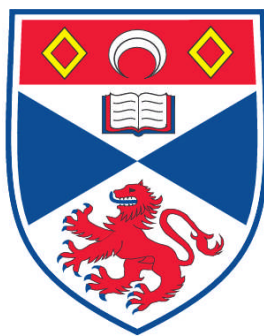


# **MULTIPLE EXPRESSIONS OF HEMISPHERIC ASYMMETRY IN CAPTIVE CHIMPANZEES**

**Stephanie Braccini**

**A Thesis Submitted for the Degree of PhD  
at the  
University of St. Andrews**



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# **MULTIPLE EXPRESSIONS OF HEMISPHERIC ASYMMETRY IN CAPTIVE CHIMPANZEES**

**Stephanie Braccini**

Thesis submitted for the degree of Doctor of Philosophy  
School of Psychology  
University of St Andrews  
September 2011

## Declaration

I, Stephanie Braccini, hereby certify that this thesis, which is approximately 40,000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

Date

Signature of candidate

I was admitted as a research student in September 2006, and as a candidate for the degree of Psychology in September 2006; the higher study for which this is a record was carried out in the University of St Andrews between 2006 and 2011.

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## **Abstract**

The degree to which non-human primate behaviour is lateralized, at individual or population levels, remains controversial and over the last century, the issue of brain lateralization in primates has been extensively researched and debated, yet no previous study has reported eye preference or head turning in great apes. This thesis examines three different expressions of hemispheric asymmetry in lateralized behaviours: hand preference for bipedal tool use, eye preference, and auditory laterality.

It is reported that bipedalism induced the subjects to become more lateralized, but not in any particular direction. Instead, it appeared that subtle pre-existing lateral biases, to the right or left, were emphasized with increasing postural demands.

Eye preference was assessed when animals looked through a hole, using one eye, at an empty box, a mirror, a picture of a dog, a rubber snake, food biscuits, bananas, a rubber duck and a video camera. Main effects of stimulus type were reported for direction of eye preference, number of looks, and looking duration, but not for strength of eye preference. A left-eye bias was found for viewing the rubber snake and a right eye bias was found for viewing the bananas. In addition, a significant shift in eye preference took place from the initial look to subsequent looks when viewing the snake. The results reported are not consistent with the literature for other primate studies.

Lastly, auditory laterality was assessed using the Hauser and Andersson (1994) head turning paradigm. Chimpanzee and American crow calls were broadcast to subjects from 180° behind them and directional head turning was recorded. No difference in

turning direction or latency was found. This lack of result was attributed to the methodology and underlying assumption that head turning is directly related to hemispheric asymmetries and not influenced by any other processes.

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## **CHAPTER 1: INTRODUCTION**

## CHAPTER 1: INTRODUCTION

The human brain is basically a paired organ; it has two halves that are almost identical in shape and size, but can be different in function. Each hemisphere of the human brain has functional specializations, meaning each hemisphere controls specific functions and tasks. For humans the most obvious and well-known specializations are speech and language. In 1861, Paul Broca identified a specific region of the left hemisphere of the brain that primarily controls speech production (Broca, 1861) and later Carl Wernicke located another control center for language comprehension, also in the left hemisphere (Wernicke, 1874). Most humans have left hemisphere language specializations, but not all; it has been estimated that approximately 96% of humans have this left hemisphere specialization, while the remaining population may have a right hemisphere specialization or possibly lack an overall lateralized specialization (Knecht et al., 2000, Pujol et al., 1999). Most recent studies indicate greater than 90% left dominance for language in human subjects.

### *Forms of Laterality*

It is well known that humans are predominantly right-handed, but there is considerable debate over other species also exhibiting laterality, defined as having a dominant side or limb. Individual preferences in side or limb have been shown in many species; including rats, chickens, elephants, whales, and even snakes for slithering direction (Bisazza et al., 1998; Clapham et al., 1995; Martin and Niemitz, 2003; Rogers, 1989; Rogers and Workman, 1993; Walker, 1980). Laterality can be

evaluated by determining which side of the body has more control relative to the other simply through observation or by utilizing more controlled methodology.

Behavioural laterality is often thought to be indicative of an underlying asymmetry of the brain (Heestand, 1986; Hopkins and Morris, 1993; Hopkins, 2007). Any behaviour that is lateralized (localized functioning attributed to the right- or left-side of the body) may be indicative of hemispheric specialization, ranging from asymmetric tail wagging in dogs (Quaranta et al., 2007), to visual laterality in dolphins (Thieltges et al., 2010), and even biases in the creation of facial expression by chimpanzees (Fernandez-Carriba et al., 2002). The most commonly examined forms of laterality are handedness, eye preference and head turning (“orienting asymmetries”).

## **Handedness**

One established and universal trait of humans is population level right-handedness (Perelle & Ehrman, 1994; Raymond & Pontier, 2004), meaning that a majority of individuals in multiple groups comprising a single population show the same hand preference within the same species. Archaeological evidence suggests the existence of human population-level hand preferences at least 2 million years ago (Cashmore, 2009; Uomini, 2009). Handedness also has a significant association with hemispheric specialization for language, with 96% of self reported right-handed humans showing a left hemisphere dominance for language, where only 70% of left-handed individuals show the same left hemisphere dominance (Knecht et al., 2000). This association has led many researchers to theorize that the

evolution of language and right-handedness are linked at some fundamental level (Annett, 2002; Corballis, 1991, 2003; McManus, 2002).

While it has been well documented that individual animals in many species display limb or hand preferences for certain tasks (e.g., Lehman, 1993; Warren, 1980), a long-running debate concerns whether a significant majority of the same group (group level preference) or multiple groups reflecting an overall species (population level preference) display the same directional preference for a given task. Hand preference has been extensively studied in non-human primates, but the results have often been inconsistent and contradictory (see Table 1.1). Primates such as bushbabies (*Galago senegalensis*, Larson et al., 1989), ruffed lemurs (*Varecia variegata variegata*, Forsythe et al., 1988) and gibbons (*Hylobates lar*, Olson et al., 1990) have been claimed to show group level left-hand preferences for bipedal food reaching. Bonobos (*Pan paniscus*) have yet to show any consistent hand preferences (D'Août et al., 2003; Chapelain and Hogervorst, 2009; Harrison and Nystrom, 2008; but cf. Hopkins 1993), while gorillas have only been suggested to have individual preferences dependent on task (*Gorilla gorilla berengei*, Byrne and Byrne, 1991; *Gorilla gorilla gorilla*, Pouydebat et al., 2010).

There are four main hypotheses regarding the origins and implications of handedness in non-human primates. The first, and most widely recognized, is the Postural Origins Theory proposed by MacNeilage et al. (1987) theorizing that laterality arose from an adaptation to unimanual predation in early primates. They reported that left-hand preferences were found for reaching while right-hand

preferences were found mainly for manipulation, suggesting that these patterns of handedness evolved with structural and functional feeding adaptations. It was suggested that the right-hand manipulative preference would strengthen as primates became more terrestrial, and in conjunction with the opposable thumb, the right-hand would become more specialized for manipulation and bimanual coordination. The left-hand would then be specialized for reaching. Hopkins et al. (2011) presents results that support this theory; the most terrestrial of the great ape species, gorillas, were reported to be the most right-handed compared to chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*) and orangutans (*Pongo pygmaeus*).

A second prominent hypothesis is the Bipedalism theory (Sanford et al., 1984), which suggests that human handedness emerged from upright bipedal locomotion. Bipedalism could have directly led to brain lateralization and in turn, handedness. Evolving from a quadrupedal posture to a less stable bipedal posture makes balance a bigger issue and could have required an increase in cerebral skills and lateralization (Falk, 1987; Sanford et al., 1984; Westergaard et al., 1998). Bipedalism frees the hands from aiding in postural support, now making them available for other activities that have been proposed to influence the emergence of handedness (e.g., gestural communication and tool use) (Bradshaw, 1993).

A third proposal is the Tool Use Theory, which proposed that handedness evolved directly as an adaptation for bimanual coordination in order to make and use tools (Provins, 1997). A similar theory links brain lateralization with the skill of throwing (Calvin, 1983). Both tool use and throwing require cognitive skill, which

may have acted as selective pressure for brain lateralization. This theory predicts that non-human primates would have a right-hand bias for tool use and throwing.

The fourth, and most recent, theory is the Task Complexity Theory. Fagot and Vauclair (1991) theorize that the strongest individual preferences and group level biases for hand use should arise from complex tasks. There are multiple factors that influence the complexity of a task: novelty, precision, accuracy, number of stages necessary to solve the task, sequence, and the need to use both hands in cooperation (Uomini, 2006). According to this theory, the more complex tasks should elicit stronger laterality than more simple tasks, and this theory is thus closely related to the tool use theory.

A majority of non-human primate laterality studies have focused on chimpanzees, both in captivity and the wild. For example, Lonsdorf and Hopkins (2005) observed that directionality of hand preference depended on the task for wild chimpanzees in Gombe: termite fishing, a coordinated bimanual task, produced a population level left-hand preference. In the Bossou, Guinea population a correlation was observed between complexity of the task performed and right-handedness (Humble and Matsuzawa, 2009). Similar correlations between strength of hand preference and task complexity have also been reported in human research (Steenhuis and Bryden, 1989). For bimanual feeding, where one hand holds the food item and the other hand brings food to the mouth, a group level right-hand bias has been reported (Hopkins, 1994). A majority of tool use studies also focus on chimpanzee subjects. McGrew and Marchant (1997, 2007) report a strong

individualized laterality for tool use, with wild chimpanzees exhibiting strong individual preference for termite fishing. McGrew and Marchant (1997) also identified conceptual and analytical problems with many claims concerning population-level handedness, leaving the fundamental debate concerning population-level handedness in chimpanzees unresolved (cf., Palmer 2002, 2003).

Handedness has been assessed in other ape species, but far less thoroughly than for chimpanzees. It has been argued that captive orangutans exhibit individual hand preferences for simple reaching and manual tool use (Colell et al., 1995; O' Malley and McGrew, 2006). Fagot and Vauclair (1988) reported a significant population level left-hand preference in food reaching tasks in captive gorillas, while a study of wild mountain gorillas failed to produce more than individual preferences (Byrne and Byrne, 1991). Individual preferences for tool use have been reported in bonobos (Harrison and Nystrom, 2008; Hopkins et al., 2011), as well as a weak lateralization for spontaneous gestures (Hopkins et al., 1993; Hopkins and DeWaal, 1995; Harrison and Nystrom, 2008), but overall there is little published regarding bonobo handedness.

The considerable differences reported both within and between species might be due to at least two pervasive factors: inconsistent testing methodology, and small sample size. To help rectify the first issue Hopkins (1994) presented a basic testing method using a bimanual 'tube' task where the subject holds a tube in one hand while extracting an object from within using the other hand. This is argued to be a strong measure given that the dominant hand will almost always be used to perform



the extraction rather than the holding (Hopkins and Cantero, 2003). This methodology has also been claimed as reliable and consistent during test-retest assessments separated by as long as 6 years (Hopkins et al., 2001).

Regarding small sample sizes, Table 1.1 presents some of the nonhuman primate literature published over the past 13 years, where over half of the sample sizes are under 20, with low effect sizes leading to inadequate power to document group or population level preferences in many studies.

Reference	Species tested	Number of subjects tested	Tasks and Results	Interpretations given by authors
Fagot and Vauclair, 1988	Gorillas	10	<ul style="list-style-type: none"> <li>• Unimanual and bimanual tasks</li> <li>• Equal handedness distribution</li> <li>• Left preference for spatial tasks</li> </ul>	Task affects hand preference, especially for reaching, novel and complex tasks.
Forsythe et al., 1988	Black and white ruffed lemurs	5	<ul style="list-style-type: none"> <li>• Food reaching</li> <li>• Left-hand preference for reaching on land</li> </ul>	Whole body postural adjustments critically influenced the expression of hand preference.

Larson et al., 1989	Lesser bushbabies	10	<ul style="list-style-type: none"> <li>• 8 conditions all requiring altered postures</li> <li>• Individual preferences (7 left and 3 right)</li> </ul>	Bipedal postures facilitated the use of the dominant hand; whereas other manipulated conditions did not have a significant affect on hand use.
Steenhuis and Bryden, 1989	Undergraduate students	942	<ul style="list-style-type: none"> <li>• Self report for variety of manual activities</li> <li>• Preference for tool use and manipulation strongly lateralized</li> </ul>	Hand preference is task dependent. Factors such as precision and heavy lifting alter lateralization.
Olson et al., 1990	Gorillas Orangutans Bonobos	12 13 9	<ul style="list-style-type: none"> <li>• Floor and mesh retrieval tasks</li> <li>• Gibbons showed left-hand preference</li> <li>• Gorillas showed right-hand preference</li> <li>• No preference shown by orangutans</li> </ul>	Posture affects hand preference, reflecting differenced in species locomotion.
Byrne and Byrne, 1991	Gorillas (wild)	44	<ul style="list-style-type: none"> <li>• Observations of natural foraging</li> <li>• Individual preferences only</li> </ul>	Hand preferences are dependent on food processing tasks
Hopkins, 1993	Chimpanzees Gorillas	40 9	<ul style="list-style-type: none"> <li>• Food reaching</li> <li>• Population preference for right-hand only for upright reaching</li> </ul>	Posture is an important factor in the exhibition of hand preference.

Hopkins et al., 1993	Bonobos	11	<ul style="list-style-type: none"> <li>• Natural observations</li> <li>• Left-hand preference for carrying</li> <li>• Right-hand preference for eating</li> </ul>	Posture is a key factor determining hand use.
Hopkins, 1994	Chimpanzees	140	<ul style="list-style-type: none"> <li>• Bimanual 'tube' task</li> <li>• Right-hand preference</li> </ul>	Using an easy bimanual task a population level right-hand preference was reported.
Colell et al., 1995	Chimpanzees Bonobos Orangutans	31 2 3	<ul style="list-style-type: none"> <li>• Food reaching task in addition to feeding observations</li> <li>• Right-hand preference for all species</li> </ul>	Postural adjustment and direction are influenced by manual laterality.
Hopkins and DeWaal, 1995	Bonobos	10	<ul style="list-style-type: none"> <li>• Variety of unimanual and bimanual tasks</li> <li>• Left-hand preference for carrying and holding food</li> </ul>	Bonobo results are consistent with those of other ape species.
Lonsdorf and Hopkins, 2005	Chimpanzees (wild)	17	<ul style="list-style-type: none"> <li>• Full day focal observations</li> <li>• Population level handedness</li> </ul>	Directionality of hand preference is task dependent. After combining all of the published data on tool use in wild chimpanzees a pattern of heritability was presented.

O'Malley and McGrew, 2006	Orangutans	8	<ul style="list-style-type: none"> <li>• Simple reaching and manual tool use</li> <li>• Individual preferences reported</li> </ul>	Hand preference is dependent on the complexity of the task.
McGrew and Marchant, 2007	Chimpanzees (wild)	37	<ul style="list-style-type: none"> <li>• Observations of ant fishing</li> <li>• No preference</li> </ul>	The evolutionary transition from a primarily arboreal species to terrestrial may have been a key enabler for the origins of human laterality.
Harrison and Nystrom, 2008	Bonobos	22	<ul style="list-style-type: none"> <li>• Tool use tasks</li> <li>• Individual preferences reported</li> </ul>	The inconstant preferences among species may be a precursor for human handedness. Species level handedness may have evolved after <i>Pan</i> and <i>Homo</i> lineage.
Chapelain and Hogervorst, 2009	Bonobos	29	<ul style="list-style-type: none"> <li>• Bimanual 'tube' task</li> <li>• Individual preferences reported</li> </ul>	Complexity of task may alter manual specialization.
Humle and Matsuazwa, 2009	Chimpanzees (wild)	31	<ul style="list-style-type: none"> <li>• 5 hand measures and 4 tool use tasks observed</li> <li>• Population level right-handedness</li> </ul>	Hand preference dependent on task and age (immature less lateralized than adults).

Pouydebat et al., 2010	Gorillas	3	<ul style="list-style-type: none"> <li>• Grasping small versus large food items</li> <li>• Individual preferences reported</li> </ul>	The complexity of the task does not necessarily induce a right-hand bias; there is considerable variability for hand preference in great apes.
Hopkins et al., 2011	Chimpanzees Gorillas Bonobos Orangutans	536 76 118 47	<ul style="list-style-type: none"> <li>• Bimanual 'tube' task</li> <li>• Population level right-handedness for chimpanzees, gorillas, and bonobos</li> <li>• Left-hand preference for orangutans</li> </ul>	Population level preferences are evident for great ape species. The species preference is a result of ecological adaptations associated with posture and locomotion.

**Table 1.1.** Summary of handedness studies with nonhuman primates in chronological order.

## Eye Dominance

Despite multiple studies on lateralization of motor function, there have been relatively few studies examining eye preference in nonhuman primates and there are currently no published studies of eye preference in apes. Eye preference, the consistent choice of one eye over the other for monocular viewing, may provide a noninvasive method for determining visual lateralization. It has now been documented in many vertebrate species with laterally placed eyes including fish

and birds (Andrew and Rogers, 2002; Vallortigara and Tommasi, 2001) and related directly to the reception and transmission of sensory information from sensory receptors to the central nervous system.

Each hemisphere of the brain does not receive sensory information from a single stimulus in the same proportions. The difference depends on species, as well as the type, amount, and speed of nerve impulse transmissions from the eye (Bishop et al., 1965). There is wide variation among vertebrate species in the degree to which information from one eye goes to one or both sides of the brain: although all vertebrates have some crossed fibers, not all have ipsilateral fibers (Jeffery & Erskine 2005). For example, most fish have fully crossed connections, so that each eye sends information only to the contralateral thalamus and optic tectum. In contrast, in many mammals, including primates, both eyes send visual sensory information to both hemispheres of the brain using the crossed fibers of the optic nerves; contralateral fibers have a larger diameter and faster conduction speed than the ipsilateral optic fibers (Watson and Hanbury, 2007), meaning that the contralateral hemisphere receives monocular visual information faster or of a higher quality than the ipsilateral hemisphere (Bishop et al., 1953; Maddess, 1975). In addition, it has been suggested that morphological asymmetries in the distribution and placement of photoreceptors and ganglion cells in the retina of each eye may result in a higher quality image being transmitted to the hemisphere contralateral to the viewing eye (Rowe, 2001; Weisz, Balaz and Adam, 1994). Because of this, eye dominance may indicate lateralization of the processing of visual information.

In our own species, directional eye dominance is not as prevalent at the population levels as handedness is, and right-eye preferences have been reported in 66.76% of humans (Bourassa et al., 1996) with more males reporting a right-eye preference than females (Reiss and Reiss, 1997). Thus motor output lateralization and sensory input lateralization are not necessarily tightly linked.

A large proportion of the visual laterality literature examines eye dominance in various fish species. At least eight species have been claimed to show a left-eye preference for looking at their own image in a mirror (*Xenotoca eiseni*, *Gambusia holbrooki*, *Xenopoecilus sarasinorum*, *Danio rerio*, *Gnatonemus petersii*, *Phoxinus phoxinus*, *Pterophyllum scalare*, *Trichogaster trichopterus*; Sovrano et al., 1999 and 2001), while mosquitofish supposedly use their right-eye to inspect a predator or other potentially dangerous object (*Gambusia holbrooki*; DeSanti, et al., 2001). Ricefish have been suggested to use the left-eye when presented with a familiar object or pattern and preferential use of the right-eye when viewing unfamiliar objects or patterns (*Oryzias latipes*; Sovrano, 2004). Additional fish species have been reported to show left-eye preferences for looking at their own image and right-eye preferences for inspecting a potential predator (DeSanti et al. 2001; Sovrano et al. 2001; Sovrano et al. 1999; Vanegas and Ito, 1983). These data suggest that familiarity or recognition may alter or influence the expression of eye preference, or possibly the emotional valence of the object being viewed.

The first primate eye preference study was conducted in 1938 with three immature capuchin monkeys (*Cebus apella*), and suggested a right-eye preference for looking

through a tube at a piece of food (Kounin, 1938). Only two studies have examined prosimians, both measuring preferences in the small-eared bushbaby (*Otolemur garnettii*). Rogers, Ward and Stafford (1994) reported that four adult females and two 1-month old bushbabies displayed left-eye preferences for viewing both the researcher and food items through a grid. This eye preference weakened when testing mother bushbabies, viewing their babies held by the researcher. Ward and Cantalupo (1997) claimed that when viewing various stimuli through a slit, 13 of 26 bushbabies (*Otolemur garnettii*) preferred the left-eye, seven preferred the right, and six subjects had no bias for either eye.

Studies examining Old World monkeys are equally inconsistent regarding eye preference; Cole (1957) noted a tendency toward right-eye preferences in a group of seven adult pig-tailed macaques for viewing food through a tube (*Macaca nemestrina*). In contrast, Kruper, Boyle and Patton (1966) reported a lack of any bias in seven adult rhesus macaques (*Macaca mulatta*), and a group bias towards left-eyedness in 19 experimentally naïve, immature rhesus macaques. Smith (1970) reported a left-eye preference in 1 naïve, immature rhesus macaque. This research, in addition to others, with naïve, immature macaques and right-eye preferences or no lack of preference in adult macaques might be taken to suggest that monocular eye use is affected by age and/or experience, but the small sample size makes interpretation risky.

There have been only four studies of eye preference in New World monkey species, also producing inconsistent results. Hook-Costigan and Rogers (1995, 1998)



propose right-eyedness in a group of 21 common marmosets (*Callithrix jacchus*) when viewing non-arousing stimuli, such as a food item. In contrast, McFerran (1992) report no overall eye preference for viewing food items and only a few individuals exhibiting eye preference in a group of 38 cotton-top tamarins (*Saguinus oedipus*). Kounin (1938) tested food viewing in three immature capuchins (*Cebus sp.*), and reported right-eye preferences. Westergaard and Suomi (1996), however, found a symmetrical distribution of eye preferences when they scored the monocular eye use of 40 capuchins (*Cebus apella*) looking through a pipe at a grape. These inconsistencies in eye preferences across primate species might reflect discontinuity in the presence and direction of lateral bias throughout primate evolution. However, these inconsistencies could also be due to small sample sizes and methodological differences across studies, including differences in age and stimulus type.

According to both the human and animal literature, visual laterality in a variety of species may vary significantly based on the emotional significance of the object being viewed and there are two general models to describe and potentially explain this: the Valence Model and the Approach-Withdrawal Model. According to the Valence Model, the expression and perception of positive emotions are produced in the left hemisphere, and negative emotions in the right hemisphere (Davidson, 1992; Ernhart et al. 1998). The Approach-Withdrawal theory postulates that that the motivation underlying approach behaviours is controlled for in the left cerebral hemisphere while those associated with withdrawal behaviours are generated in the right hemisphere (Demaree et al. 2005). Davidson and others have produced a

variety of evidence over the past 10 years indicating the two hemispheres of the brain are differentially responsible for specific positive and negative emotions. What sets these two models apart is the response behaviours and role of emotion. The Valence Model relates only to the expression and processing of emotion, positive and negative, not the behaviour that results from those emotions. While emotions such as fear and disgust can be causes or motivators to withdrawal behaviours, the Approach-Withdrawal Model only concerns itself with the drive to move towards or away from an object or situation. Withdrawal entails physically moving away from a threatening stimulus, whereas in disgust the withdrawal entails ending the interaction, be it olfactory, oral or visual (Ekman & Friesen 1975).

Previous research suggests that changes in eye preference are a function of stimulus type and/or level of arousal in nonhuman primate species. Bushbabies (*Otolemur garnettii*, Rogers et al. 1994), marmosets (*Callithrix jacchus*, Hook-Costigan & Rogers, 1998), and mangabeys (*Cercocebus torquatus*; de Latude et al., 2009) have all been proposed to exhibit differential monocular eye use as a function of stimulus type. As previously mentioned, five bushbabies displayed left-eye preferences when viewing food, but when three of the same subjects viewed a more arousing stimulus (their own babies held in the experimenter's hand) two displayed no eye preference and the third displayed a weaker left-eye preference (Rogers et al. 1994). A group level bias for right-eyedness was implied for 21 common marmosets when viewing stimuli that did not elicit negative emotional responses (e.g., vocalizations indicative of arousal; Hook-Costigan & Rogers, 1998). However, when the same

marmosets viewed a threatening stimulus, a model resembling two rearing snakes, they reportedly displayed increased arousal (increased incidence of aroused vocalizations), and also showed shifts in eye preference from a right-eye preference to no preference or a left-eye preference. Combined, these data strongly suggest that eye preferences may reflect differential hemispheric specializations for perceptual processing that are dependent on the emotional valence of the stimulus.

Given that laterality might be reflective of an overall side preference, which has been proposed as a unified underlying mechanism of both hand and eye preference (Bourassa et al., 1996; Porac, 1997), the relationship between hand preference and eye preference has also been explored. Hand and eye preference show some association in humans, with increased incidence of left-eye preferences among left-hand preferent humans (Bourassa et al., 1996; Porac, 1997). However, the majority of the nonhuman primate literature presents little to no relationship between the two measures (Cole, 1957; Hook-Costigan & Rogers, 1998; Kruper et al. 1966; Rogers et al. 1994; Westergaard & Suomi, 1996;). Ward and Cantalupo (1997) are the only authors to claim a positive correlation between eye and hand preferences. This relationship was present, however, only for a subset of the bushbabies tested, comprised of individuals that showed different hand preferences when reaching in to a jar from a tripedal and bipedal posture. Nevertheless, the relationship between sensory and motor lateralization should be evaluated to determine if a common mechanism underlies lateralized motor or perceptual control in nonhuman primates, as well as humans.

Reference	Species tested	Number of subjects tested	Stimuli and Results	Interpretations given by authors
Miles, 1930	Humans	600	<ul style="list-style-type: none"> <li>• Various eye preference tasks and handedness self report</li> <li>• 64% R-eyed</li> <li>• 34% L-eyed</li> <li>• 2% no preference</li> <li>• No hand-eye relation</li> </ul>	Right-handed humans had a higher report of right-eye preference than left-handed humans implying a similar operating process.
Kounin, 1938	Rhesus macaques, Spider monkey. Cebus monkeys	4 1 3	<ul style="list-style-type: none"> <li>• Viewing food through a tube</li> <li>• Individual eye preference</li> <li>• No hand-eye relation</li> </ul>	Hand preference was task dependent and related to greater tendency towards investigation and manipulation.
Cole, 1957	Pig tailed macaques	7	<ul style="list-style-type: none"> <li>• Viewing food through a tube</li> <li>• L-eye preference</li> <li>• No hand-eye relation</li> </ul>	Although crossed laterality in the limbs is exceptional, it is not related to eye dominance.
Smith, 1970	Rhesus macaques	1	<ul style="list-style-type: none"> <li>• Binocular viewing</li> <li>• Left-eye preference</li> <li>• Left-hand preference</li> </ul>	Ocular dominance and hand preference are related and possibly a distinguishing trait of rhesus.
Kruper, Boyle, and Patton, 1966	Rhesus macaques	19	<ul style="list-style-type: none"> <li>• Viewing food through a mounted tube</li> <li>• Group level L-eye preference</li> <li>• Individual hand preferences</li> </ul>	Lack of correlation between hand and eye preference suggests preferences are not mediated by a simple common factor.

McFerran, 1992	Cotton top tamarins	38	<ul style="list-style-type: none"> <li>• Food viewing through hole</li> <li>• No eye bias, slight individual preferences</li> </ul>	The subjects had either a left-eye preference or no preference suggesting some adaptive quality for tamarins independent of other primates.
Rogers, Ward and Stafford, 1994	Bushbabies	6 (4 adults and 2 1-month old babies)	<ul style="list-style-type: none"> <li>• Viewing various stimuli through a grid</li> <li>• Group level L-eye preference</li> <li>• No correlation with handedness</li> </ul>	Increased arousal, or fear, altered eye preference suggesting lateralization for both processes.
Hook-Costigan and Rogers, 1995	Common marmoset	8	<ul style="list-style-type: none"> <li>• Trained to look through a slit</li> <li>• Group level right-eye preference</li> <li>• No correlation with individual handedness</li> </ul>	Eye preference, independent of other motor behaviours, represents an independent form of hemisphere specialization, possibly related to perceptual processing.
Westergaard and Suomi, 1996	Capuchin monkeys	48	<ul style="list-style-type: none"> <li>• Food viewing through a hole</li> <li>• No group level bias, but strong individual bias</li> </ul>	Distribution was symmetrical, suggesting equal adaptive advantages for both eyes.
Porac, 1997	Humans	387	<ul style="list-style-type: none"> <li>• Self report for eye preference and handedness</li> <li>• Strong individual preferences for eye and hand</li> <li>• L-eye preference more frequent with L-hand</li> </ul>	Results are consistent with idea of a common mechanism underlying limb and eye lateral preferences, but unknown which is driving force.

Hook-Costigan and Rogers, 1998	Common marmoset	21	<ul style="list-style-type: none"> <li>• Viewing food through a hole</li> <li>• Group level right-eye preference</li> <li>• No relationship with handedness</li> </ul>	Eye preferences may reflect hemispheric specializations for perceptual processing, according to the emotional valence of the stimulus.
Sovrano et al., 1999	Eastern mosquitofish, Redtail splitfin, Common minnow, Sarasins minnow, Angelfish, Labyrinth fish	20	<ul style="list-style-type: none"> <li>• Inspection of own image</li> <li>• Left-eye preference for females</li> <li>• No preference for males</li> </ul>	Males could be induced to manifest a left-eye preference soon after capture, implying the role of capture and captivity on the expression of laterality.
DeSanti et al., 2001	Mosquitofish	32	<ul style="list-style-type: none"> <li>• Inspection of own image</li> <li>• Left-eye preference</li> <li>• Predator inspection</li> <li>• Left-eye preference for viewing at a distance and right-eye when near the predator</li> </ul>	Eye preference is dependent on what is being viewed, distance of viewing and environment, suggesting complex lateralization for various factors.
Sovrano et al., 2001	Sarasins minnow, Eastern mosquitofish, Red-Tailed Goodeid, Zebrafish, Elephantnose fish	93	<ul style="list-style-type: none"> <li>• Inspection of own image</li> <li>• Left-eye preference only during first five minutes of observation</li> <li>• </li> </ul>	Results claim invariant pattern to the direction of lateralization with preferential involvement of structures located to the right side of the brain in response to the viewing of conspecifics.

Sovrano, 2004	Sarasins minnow	24	<ul style="list-style-type: none"> <li>• Inspection of own image</li> <li>• Left-eye preference</li> <li>• Artificial stimuli</li> <li>• Left-eye preference for familiar orientation, right-eye for unfamiliar</li> </ul>	Preferential use of the monocular visual field is most likely part of a more generalized specialization for determining identity or visual response control.
Chapelain and Blois-Heulin, 2008	Campbell's monkeys	14	<ul style="list-style-type: none"> <li>• Food viewing through tube</li> <li>• 8 Right-eyed</li> <li>• 6 Left-eyed</li> </ul>	Early emergency of lateralization for perceptual processing compared to manual motor functions explains eye preference in the absence of other limb preferences.
deLatude et al., 2009	Red-capped mangabeys	14	<ul style="list-style-type: none"> <li>• 2 methods (tube and box) with 5 different stimuli</li> <li>• Group level left-eye preference</li> </ul>	Palatability of stimuli affected preferential eye use supporting the theory of valence and a hemispheric processing of emotion.

**Table 1.2.** Summary of studies examining eye preference, in chronological order.

## Ear Preference / Head Turning Asymmetries

A left hemisphere dominance for the processing of spoken language in humans has been clearly established over the past century (Belin et al., 1998; Bethmann et al., 2007; Fischer et al., 2009; Geschwind, 1970; Geschwind and Levitsky, 1968)

suggesting that the left cerebral hemisphere of the human brain is more involved than the right in both the production and perception of speech sounds (Petersen et al., 1978). Building upon this known bias, animal researchers have sought the evolutionary roots of left lateralization, producing some interesting, but inconsistent, results suggesting that the lateralization of processing acoustic stimuli is not exclusive to humans, but shared with at least some nonhuman primates and other vertebrates.

Numerous studies have suggested that rhesus macaques (Agnetta, and Perez, 1998; Ghazanfar, Smith-Rohrberg, and Hauser, 2001; Hauser and Andersson, 1994), Japanese macaques (Beecher et al., 1979; Petersen et al., 1978), and sea lions (Böye, Güntürkün and Vauclair, 2005) all show varying degrees of left hemisphere dominance. Various exceptions have been noted, with vervet monkeys showing right dominance (Gil-da-Costa and Hauser, 2006) and Barbary macaques showing no dominance (Teufel, Hammerschmidt, and Fischer, 2007) suggesting that auditory laterality when processing conspecific communication may be affected by various factors and/or afflicted with various methodological problems. Table 1.3 provides an overview of these studies.

Factors influencing auditory laterality include emotional valence, which has been suggested to alter orienting biases in dogs (Siniscalchi, Quaranta, and Rogers, 2008) and Campbell's monkeys (Basile, Lemasson, and Blois-Heulin, 2009) where stimuli that elicit a negative emotional result are suggested to be processed preferentially by the right hemisphere. The opposite case has also been argued,



with male mouse lemurs displaying a left hemisphere dominance for processing sounds with negative emotional content (Scheumann & Zimmermann, 2008).

In addition to emotional valence, communicative significance has been suggested to affect laterality in Japanese macaques, with a left hemisphere preference being shown for familiar and “meaningful” calls (Petersen et al., 1978; Petersen et al., 1984). Campbell’s monkeys have also been claimed to respond differentially based upon familiarity: Basile, Lemasson, and Blois-Heulin (2009) compared Campbell’s monkeys to human 8- and 9-year old girls (where a right-turn bias was reported in response to negative context vocalizations produced from an unfamiliar conspecific, but no bias was reported for positive valence vocalizations). Campbell’s monkeys also failed to exhibit any bias towards positive vocalizations, but did display a left bias for species-specific negative vocalizations.

The caller, or source of the vocalization, has been claimed to affect laterality depending on species. Barbary macaques were tested with two different species-specific calls and three different heterospecific calls, but no significant orienting difference was reported (Teufel et al., 2007). Mouse lemurs also failed to show any asymmetry, of a same or different direction, to various conspecific and heterospecific calls (Scheumann and Zimmermann, 2008). A left turn bias was reported in vervet monkeys in response to species-specific vocalizations, but no bias was reported in response to heterospecific vocalizations or non-biological sounds (Gil-da-Costa and Hauser, 2006). Lemasson et al (2010) reported similar findings for Japanese macaques, with a left-turn bias suggested in response to

species-specific calls but not for non-biological sounds. Domestic dogs (Siniscalichi et al., 2008), California sea lions (Böye et al., 2005) and domestic horses (Basile, Boivin, et al., 2009) also have been theorized to exhibit a right-turn bias in response to conspecific vocalizations, but not to heterospecific or vague stimuli.

The human literature has proven equally inconsistent, as highlighted by Fischer et al. (2009). In a comparison between human behavioural orienting asymmetries and fMRI results, it was suggested that in humans, orienting biases are not necessarily accurate reflections of lateralizing processing of acoustic stimuli. This is based on the lack of significant turning biases reported for the orienting asymmetries, which contradicts the clear left hemisphere activation for human speech that was observed via fMRI. This finding calls into question the underlying assumption of most previous studies, namely that there is a clear connection between neural lateralization and the head-turn response.

A serious confounding factor in these studies of orienting asymmetries is testing methodology. The most popular non-invasive indicator of auditory laterality in animals is the head turn paradigm first described by Hauser and Andersson (1994) for rhesus macaques. This test requires that an auditory cue be broadcast from behind a subject. The side to which the subject rotates or looks is then recorded. The key assumption being that since both ears receive the same auditory cue, turning to one side intensifies the input and potentially creates a biased input of further acoustic information to the contralateral hemisphere. However Teufel et al

(2010) argue persuasively that several of the assumptions underlying this assay are invalid. An overview of the studies utilizing this method shows an inconsistent pattern of results and largely *ad hoc* set of interpretations, varying considerably across species and studies (see Table 1.3).

These studies all rely on one fundamental, yet largely untested, assumption that one hemisphere is preferentially activated during the processing of a specific acoustic signal, and that this activation is seen as a turning bias. Given that Fischer et al. (2009) were unable to directly correlate the relationship between lateralized acoustic processing and orienting asymmetries in humans it seems doubtful that this fundamental assumption of the orienting asymmetry paradigm is accurate.

References	Species tested	Number of subjects tested	Stimuli and Results	Interpretations given by authors
Hauser & Andersson (1994)	Rhesus macaques	10-41	<ul style="list-style-type: none"> <li>• Species-specific affiliative, fearful, aggressive calls result in R-turn bias in adults, but not infants</li> <li>• Heterospecific alarm call of ruddy turnstone. Result in L-turn bias in adults, but not infants</li> </ul>	Adult, but not infant, rhesus macaques process conspecific calls in the left hemisphere and heterospecific calls in the right hemisphere.

Hauser et al. (1998)	Rhesus macaques	7-19	<ul style="list-style-type: none"> <li>• Species-specific affiliative, alarm, mating calls</li> <li>• Temporarily manipulated affiliative and alarm calls resulting in left-turn bias or no bias</li> <li>• Temporarily manipulated mating call resulting in right-turn bias</li> </ul>	Temporal cues are used to classify affiliative and alarm calls, but not mating calls as conspecific.
Ghazanfar & Hauser (2001)	Rhesus macaques	10-20	<ul style="list-style-type: none"> <li>• Species-specific alarm and food calls</li> <li>• Resulted in right-turning bias</li> <li>• Time reversed alarm calls and food calls</li> <li>• Resulted in left-turning bias</li> </ul>	Temporal cues are used to classify alarm and food calls as conspecific.
Palleroni & Hauser (2003)	Harpy eagles	4 captive, 3 wild	<ul style="list-style-type: none"> <li>• Species-specific contact calls</li> <li>• Right-turn bias</li> <li>• Heterospecific call of a potential prey</li> <li>• Wild eagles displayed right-turning bias</li> <li>• Captive eagles displayed a left-turning bias</li> </ul>	Left hemisphere auditory processing is determined by hunting experiences.

Böye et al. (2005)	California sea lions	6 adult, 2 infants	<ul style="list-style-type: none"> <li>• Familiar and unfamiliar species-specific calls</li> <li>• Reported right-turn bias in adults but not infants</li> <li>• Familiar and unfamiliar heterospecific calls</li> <li>• No bias reported for adults or infants</li> </ul>	Adults, but not infants, process species-specific sounds in the left hemisphere.
Gil-da-Costa & Hauser (2006)	Vervet monkeys	4-5	<ul style="list-style-type: none"> <li>• Various species-specific vocalizations produced by familiar and unfamiliar individuals</li> <li>• Left-turning bias reported</li> <li>• Familiar and unfamiliar heterospecific vocalizations from various primate species</li> <li>• No bias was reported</li> <li>• Non-biological sounds failed to produce a bias</li> </ul>	Vervet monkeys process species-specific calls in the right hemisphere, indicating that asymmetries in acoustic processing are a general principle of the primate brain but the direction of this asymmetry is plastic.
Teufel et al. (2007)	Barbary macaques	19-36	<ul style="list-style-type: none"> <li>• Various species-specific and heterospecific calls</li> <li>• No bias reported</li> </ul>	Authors questioned the validity of the orienting paradigm to track lateralized acoustic processing.

Scheumann & Zimmermann (2008)	Grey mouse lemurs	20-28	<ul style="list-style-type: none"> <li>• Species-specific calls with positive valence</li> <li>• No turning bias reported</li> <li>• Species-specific calls with negative valence</li> <li>• Females did not exhibit any preference</li> <li>• Males showed a right-turning bias</li> <li>• No turning bias for various heterospecific calls</li> <li>• No turning bias for non-biological sounds</li> </ul>	A sex specific left hemisphere lateralization for acoustic processing of species-specific calls with a negative valence.
Fischer et al. (2009)	Adult humans	<p>22 Paired adults in a lab</p> <p>40-63 Independent field study</p>	<ul style="list-style-type: none"> <li>• Functional MRI response lateralized to left hemisphere in response to speech stimuli</li> <li>• Species-specific speech sounds</li> <li>• Left-turn bias reported for 1 sample (Germany), but not the other (UK)</li> <li>• No turning bias reported for non-biological sounds</li> </ul>	There is no direct relationship between lateralized acoustic processing and asymmetries for orienting behaviours.

Basile, Lemasson, et al. (2009)	Campbell's monkeys Human girls (8-9 years old)	7 monkeys  13 girls	<p>Monkeys:</p> <ul style="list-style-type: none"> <li>• Species-specific calls, positive and negative valence</li> <li>• No turning bias reported</li> <li>• Heterospecific calls with negative valence</li> <li>• No turning bias reported</li> </ul> <p>Human Girls:</p> <ul style="list-style-type: none"> <li>• Familiar and unfamiliar species-specific vocalizations, both positive and negative</li> <li>• Right-turning bias for negative valence vocalization by familiar classmate</li> <li>• No other biases reported</li> </ul>	Lateralized auditory processing exists only for familiar vocalizations with a negative valence, Campbell's monkeys processing is lateralized to the right hemisphere while human girls process in the left hemisphere.
Lemasson et al. (2010)	Japanese macaques	5-6	<ul style="list-style-type: none"> <li>• Familiar species-specific contact calls</li> <li>• Left-turning bias reported</li> <li>• Familiar chimpanzee calls</li> <li>• Left-tuning bias reported</li> <li>• Additional familiar primate and familiar non-biological sounds</li> <li>• No bias reported</li> <li>• Various unfamiliar primate and non-biological calls</li> <li>• No bias reported</li> </ul>	Japanese macaques process species-specific and some other familiar sounds in the right hemisphere, indicating that lateralized auditory processing is influenced by previous experiences.

**Table 1.3.** Summary of studies utilizing the orienting asymmetry paradigm, in chronological order.

## **Additional Forms of Laterality**

In addition to the previously discussed expressions of laterality, footedness and nipple preference have both been documented in great apes. Nishida (1993) reported a left side bias in nipple preference in a sample of 32 wild chimpanzees, with approximately 64% of the sample showing the preference. No relationship was reported between teat preferences and hand preference for touching objects and holding food. Female chimpanzees and gorillas show a left side cradling bias, which only compliments their overall right-hand bias (Hopkins, 2004). It is not known if the asymmetries in cradling or nipple preference are associated with hand preference of the individuals. It seems logical that right-handed individuals would want to keep the right hand free for other tasks or locomotion, leaving the left hand available for cradling. Great ape infants also appear to show a left side positional bias on females, as well a left nipple preference. It is not clear though if there is a bias by the mother imposed on the offspring or if the mother is accommodating the bias of the infant. Additional research has shown that neonatal (birth to 90 days of age) chimpanzees have significantly stronger grips in the right hand and foot versus the left (Fagot and Bard, 1995). Neonatal chimpanzees have also been reported to show a right side bias in leading limb during locomotion in both captive and wild populations (Chorazyna, 1976; Hopkins, Bard and Griner, 1997; Cunningham, Forsythe, and Ward, 1989).

For humans, most people have uncrossed lateral preferences, meaning that they prefer the foot ipsilateral to their hand. However, between 1.5% and 6% of right-handed adults appear to prefer their left foot when initiating movement (Elias,



Bryden, and Bulman-Fleming, 1998). The preference for crossed lateral preference is higher in left-handed individuals with between 20% and 50% preferring their right foot (Day and MacNeilage, 1996). Given the prevalence of right-handedness reported for captive chimpanzees, a right-limb preference would be expected. Both Heestand (1986) and Harrison and Nystrom (2008) reported right limb asymmetries for great apes, including captive chimpanzees. Marchant and McGrew (1996) however found no evidence of a population level leading limb preference in wild chimpanzees. Hopkins (2008) looked closer at the asymmetries and reported a population level left bias in descending locomotion and no bias for ascending. Interestingly, he did find that older subjects were more lateralized in locomotor movement than younger apes and males were more lateralized than females. The discrepancies in reports could very well be due to differences in defining “leading limb” and in methodology. In both Heestand (1986) and Harrison and Nystrom (2008) leading limb was operationally defined as the limb that led out during level locomotion from a quadrupedal posture, while Heestand (1986) also reported climbing leading limb collapsing ascending and descending preferences. To date no reports have postulated why some humans, or apes, have ambi-preference for footedness and what that might mean.

### ***Thesis Aims and Scope***

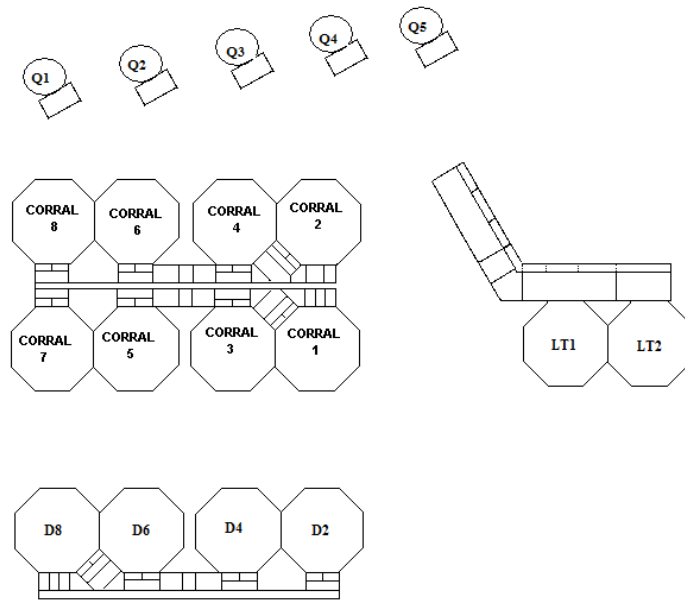
The animal laterality literature presents a complex and confusing picture, marred by small sample sizes and inconsistent methodologies, making it very difficult at present to draw any firm evolutionary conclusion about the origins of human laterality. One crucial comparison for understanding the evolution of human

laterality is that between humans and our closest living cousins, chimpanzees. Despite a considerable number of studies on chimpanzee handedness, reviewed above, there is a surprising shortage of research on sensory laterality, whether visual or auditory, in chimpanzees or other great apes.

The present thesis aims to begin filling in this gap, and includes three studies on lateralization in the common chimpanzee *Pan troglodytes*. The first examines the role of posture in a tool use task, and replicates and extends previous work on the handedness in chimpanzees. The second study is the first to examine eye preferences in chimpanzees, and employs a variety of stimuli chosen to represent various levels of arousal and familiarity. The third study examined auditory laterality, using a head turn paradigm and conspecific versus heterospecific vocalizations. In all of these cases, a large sample size of captive chimpanzee subjects was used, and consistent, rigorous methodologies from the literature were employed to allow better comparisons across studies and species.

All studies were conducted at Michale E. Keeling Centre for Comparative Medicine and Research of The University of Texas MD Anderson Cancer Centre in Bastrop, Texas. The facility has eight open top corrals and 11 Prima-domes, each providing both indoor and outdoor housing. Each corral houses between six and fourteen animals, while each dome houses between three and six animals (see Figure 1.1). Support for all projects presented in this thesis came from NIH/NCRR U42-RR15090. All procedures were conducted in accordance with all relevant federal,

state, and local guidelines and were approved by the UTMDACC IACUC. This facility is fully accredited by AAALAC-International since 1979.



**Figure 1.1.** An overview of the Michale E. Keeling Centre for Comparative Medicine and Research, Department of Veterinary Sciences, University of Texas M.D. Anderson Cancer Centre in Bastrop, Texas.

As noted at the beginning of some chapters, the data therein have been submitted for publication. I carried out all testing, coding and analyses involved in the research. As first author, I wrote all the manuscripts that were submitted, and additional authors were the lab supervisors and my advisor who supervised the experiments and contributed feedback on subsequent revisions of the manuscripts.

## **CHAPTER 2: BIPEDAL TOOL USE STRENGTHENS CHIMPANZEE HAND PREFERENCES**

The data in this chapter were published in:

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## **CHAPTER 2: BIPEDAL TOOL USE STRENGTHENS CHIMPANZEE HAND PREFERENCES**

### ***INTRODUCTION***

One characteristic that distinguishes humans from other primates is that a substantial majority of humans, close to 90%, are right-handed (Gilbert and Wysocki, 1992; Perelle and Ehrman 1994). A species level bias of this magnitude has not been found in any other primate species. Despite considerable disagreement as to how handedness should be defined or measured, the handedness of multiple primate species has been evaluated in a variety of tasks. Handedness is one component of the concept of laterality (having a behaviourally dominant side or limb) often presumed to be indicative of asymmetry of the brain (Heestand, 1986; Hopkins and Morris, 1993; Hopkins, 2007). Laterality can be evaluated by determining which side of the body has more control relative to the other, or by determining which side of the brain is more responsible for specific actions or behaviours. Individual laterality and side preferences have been shown in various species, including rats, chickens, elephants, whales, and even snakes (Bisazza et al., 1998; Clapham et al., 1995; Martin and Niemitz, 2003; Rogers, 1989; Rogers and Workman, 1993; Walker, 1980).

Primates and other vertebrate species show laterality of function, but no other primate species shows such a marked or extensive cerebral asymmetry at a population level as humans (Vallortigara and Rogers, 2005). Laterality is therefore often thought to have played an important role in the evolution of human cognition. Speech is typically lateralized to the left hemisphere of the human brain, but can occasionally be expressed

in the right hemisphere (Knecht et al., 2000). Apes do not exhibit spoken language, but if they do display laterality, it probably reflects a trait present in the last common ancestor of humans and other great apes, and this trait may have acted as a pre-adaptation in the evolution of language (Hopkins and Cantero, 2003; Steele and Uomini, 2009; Vallortigara and Rogers, 2005). Other lateralized behaviours hypothesized to have influenced the evolution of cognition include tool use (Gibson and Ingold, 1993; Preston, 1998), manual gestures (Corballis, 2003; Hopkins and Leavens, 1998; Pollick and de Waal, 2007; Rizzolatti and Arbib, 1998), and throwing (Hopkins et al., 1993; Hopkins et al., 2005). Furthermore, posture has been shown in some previous studies to influence handedness (Hopkins and Morris 1993; Roney and King, 1993), with upright or bipedal postures increasing right-handedness, suggesting a need to evaluate the effects of tool use and bipedal posture concurrently.

The aim of the present study was to examine the relationship between hand preference and posture during a tool use task in captive chimpanzees. The task demands were manipulated so that the tool-use could be accomplished 1) while seated, 2) while bipedal but with one hand against a wall, and 3) while fully bipedal. The main goals were to test the prediction that assumption of bipedal posture would increase the strength of right-hand hand preference during tool use. Based on the existing literature, two hypotheses were tested: H1) bipedal posture increases the **strength** of hand preference, without respect to side, and H2) more specifically, a bipedal stance, without the use of one hand for support, elicits a **right-hand** preference.

These two hypotheses need to be distinguished because previous work in nonhuman animals shows that a group of animals may differ in laterality overall (that is, some animals in a group may be ambidextrous, while others are strongly lateralized, but with equal numbers of left- and right-lateralized individuals). Such lateralized individuals might still lack any group- or population-level directional bias to use the *right*-hand. Humans, of course, are both lateralized (ambidextrous individuals are rare) and directionally lateralized to the right side (left-handed individuals are equally rare), but these two characteristics need not go together. These two logical possibilities are distinguished between by calculating, for each subject, both a handedness index (ranging from 1.0 to -1.0, and whose sign reveals the directional bias to the right or left respectively) and an *absolute* handedness index (ranging from 0.0 for ambidextrous, to 1.0 for strongly lateralized animals which use either the left or right-hand exclusively).

## ***METHODS***

### **Subjects & Housing**

For this experiment, 46 chimpanzees (28 males and 18 females) ranging in age from 12 to 47 years (mean age of 28.15 years) of various subspecies (mostly *Pan troglodytes verus*) were used. The chimpanzee subjects used in this experiment were housed at the Michale E. Keeling Centre for Comparative Medicine and Research at The University of Texas M.D. Anderson Cancer Centre in Bastrop, Texas (MDACC). The facility has eight open top corrals, each providing both indoor and outdoor housing to 7-14 animals per group. All chimpanzees remained in their home corrals for testing. Subjects were chosen from all corrals to be included in all experimental conditions. Subjects were

also chosen based on their inclusion in previous handedness studies and included 15 right-handed, 16 left-handed, and 15 ambidextrous individuals (Hopkins et al, 2003). These animals all have considerable experience extracting food from tubes, due to both frequent enrichment (pipe feeders are provided on a weekly basis which require tools to be inserted into fixed pipes to extract various food substances) and previous exposure to a similar task (Hopkins et al, unpublished data).

## **Apparatus**

A poly-vinyl-chloride (PVC) tube (135 cm in length, 4 cm in diameter) with peanut butter in the centre was suspended in an outdoor enclosure using 80 lb test fishing line connected to an eyelet in the cap of the tube. Fishing line was used so that each time a chimpanzee grabbed hold of the food tube and pulled downwards, the line broke, ensuring that the animals could not climb up the line and escape their enclosure. In the event that a chimpanzee jumped and grabbed the tube, the researcher returned to ground level and recovered the tube, cap, and broken line. In order to better maintain a consistent distance, the fishing line was strung through a 1.35 m PVC tube and secured (Figure 2.1). The food tube was lowered into the enclosure until it was approximately 2.8 m off the ground, which is the total of the average height of an adult chimpanzee (150 cm), the average length of a chimpanzee arm (83 cm), and the length of the tool (45 cm). The distance of the food tube from the interior walls of the corral differed based on experimental condition.





**Figure 2.1.** Peanut butter tube suspension apparatus viewed from the side. The tube about to be put into the corral is in front of the suspension system and the fishing line is run through the larger PVC and wrapped around the top extension to secure it.

## Procedure

All subjects participated in all three of the experimental conditions, first in the seated condition (data collected in 2002), then the supported bipedal conditional, the bipedal condition, and finally in a retest of the seated condition. The initial seated data was used to allocate individuals to three groups of equal size (of left- handed, right-handed, and ambidextrous individuals). For all conditions, trials were run daily, with a minimum of 36 hours between trials for any particular group. All trials took place in the outdoor section of the subject's home corral and subjects from each corral were tested. Research in a particular corral lasted at least 2 hours in order for all focal animals to have the opportunity to gain access.

Each trial, regardless of condition, began with the researcher placing cut bamboo sticks (45 cm long) within reach of every member of the test group. The subjects then

gathered these tools, without any restriction on the hand used to take the stick. PVC tubes with peanut butter smeared in the centre (near to the midpoint of the tube's axis) were provided to the chimpanzees along with tools in the form of the cut bamboo sticks. Peanut butter was placed only in the centre of the tube to encourage tool use and prevent subjects from using their hands to extract the peanut butter.

## **Data collection and analysis**

Data for all sessions were recorded on a Dictaphone via spoken commentary. The term 'event' was used to designate one instance of feeding (e.g., inserting the tool into the tube, pulling out the tool, inserting the tool into the mouth, and repeating) and trials continued until the focal subjects in each group had displayed at least 50 events, over a minimum of three testing trials. 'Bouts' were groups of events, which either occurred on different days, or in which the subject put down the tool, left the test apparatus, and later returned during a single test session. "Bout-wise" data were scored using only the first event of each bout as independent data points, while "event-wise" analyses incorporated all events as data points. In order to meet the designated minimum of 50 events, between 3 and 11 data collection trials were completed by the chimpanzees, during which the chimpanzees completed 50 to 72 events. Between 3 and 11 (mean of 4.95) independent 'bouts' were scored as single data points for the bout-wise HI.

*Handedness Indices* for all animals were calculated to quantify the degree of lateral bias. This was done by subtracting the number of left hand uses (L) from the number of right-hand uses (R), and dividing by the total number of hand use instances (R + L):

$$HI = \frac{R - L}{(R + L)}$$

HI values range from 1.0 (extreme right-handed) to -1.0 (extreme left-handed).

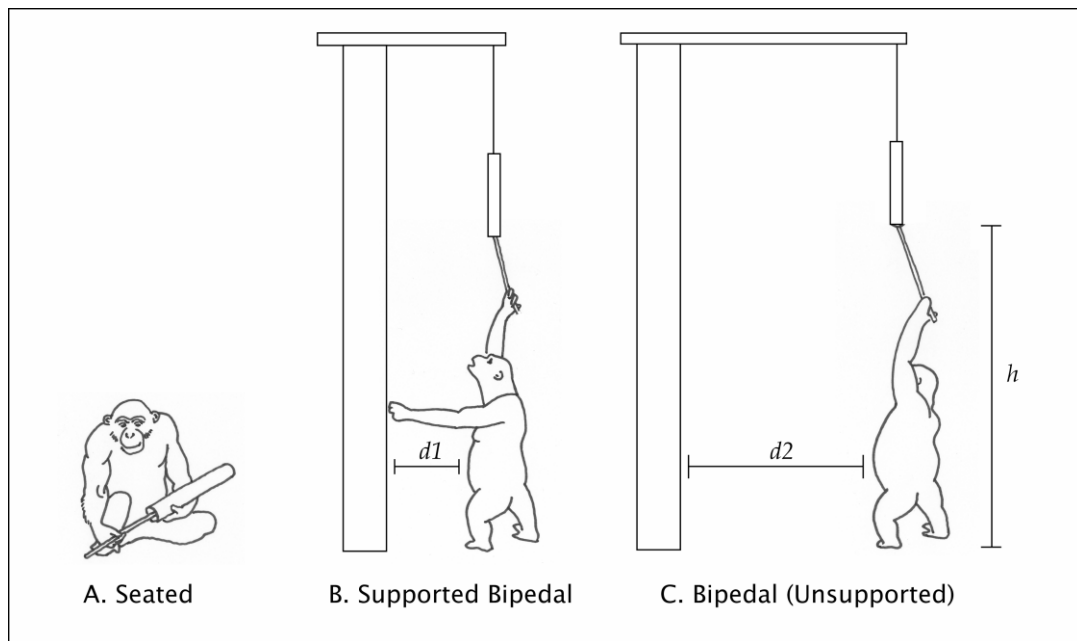
*Absolute Handedness* was also calculated (absolute HI = |HI|); the absolute value of the HI score represents the strength of hand preference irrespective of direction and ranges from 0 (ambidextrous) to 1.0 (extreme lateralization in either direction). Statistical analysis was conducted using JMP software version 8.0.1 and SPSS software version 16.

Subjects' posture was experimentally manipulated in the following three conditions:

Seated condition (SC): This condition was run twice, first to assign animals to groups, and again after all other trials, in order to re-assess baseline hand preference. Here the chimpanzee was allowed to hold the food tube; in this situation all chimpanzees sat down before extracting the peanut butter (Figure 2.2A).

Supported bipedal condition (SB): From the roof of the corral, the food tube was positioned within reaching distance of the coral wall (approximately 75 cm away), allowing the subject to use one hand to perform the tool use task and the other to provide postural support by bracing themselves against the wall (Figure 2.2B). The researcher remained on the roof for the duration of the trial in order to lower and raise the apparatus as needed in order to prevent the tubes from being pulled into the enclosure.

Bipedal condition (B): The method used for this condition was identical to that of the supported bipedal condition test, with only one exception. For this experimental condition, the tube was suspended approximately 1 m away from the wall so that the subjects could not use their hand to support themselves against the wall, forcing them to adopt an unsupported bipedal posture (Figure 2.2C).



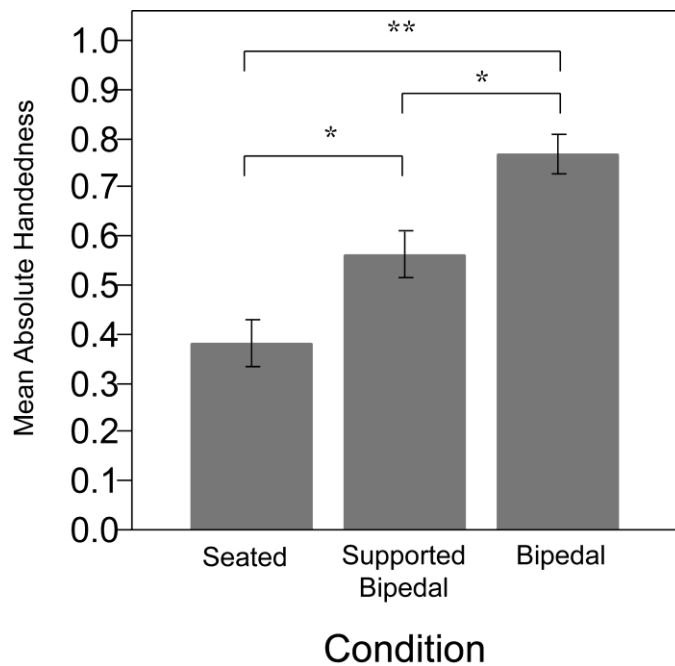
**Figure 2.2.** Sketch of a chimpanzee performing the task for each condition. A) Baseline condition: seated tool use. B) Supported bipedal condition: bipedal tool use while using one arm for support. C) Bipedal condition: completely bipedal tool use without any support. Measurements indicated are  $d1$ : 75 cm maximum,  $d2$ : 100 cm minimum,  $h$ : 2.8 m. (Figure by WTF).

## RESULTS

No significant deviation from normality was found (Kolmogorov-Smirnoff test,  $p > 0.05$  for all conditions), for either Handedness Index (HI) or the absolute HI (abs HI). Thus we used parametric ANOVAs to examine these data.

## Strength of hand preference

To evaluate the effect of posture on the strength of hand preference, we examined the absolute values of each subject's HI, as calculated from each event (Figure 2.3). A repeated measures ANOVA with postural condition as the independent variable and the absolute value of the HI set as the dependent variable yielded a significant main effect for postural condition ( $F [2, 44] = 37.012, p < 0.001$ ). A Tukey post hoc analysis indicated that the mean absolute HI significantly increased from the seated condition to the supported bipedal condition ( $p = 0.019$ ), from the supported to the bipedal condition ( $p = 0.004$ ), and from the seated to the bipedal condition ( $p < 0.001$ ). A non-parametric Wilcoxon signed ranks test was also performed in order to confirm previous results, yielding significant results (seated to supported condition  $Z = -2.71, p = 0.007$ ; supported to bipedal condition  $Z = -3.64, p < 0.001$ ; seated to bipedal condition  $Z = -4.76, p < 0.001$ ).



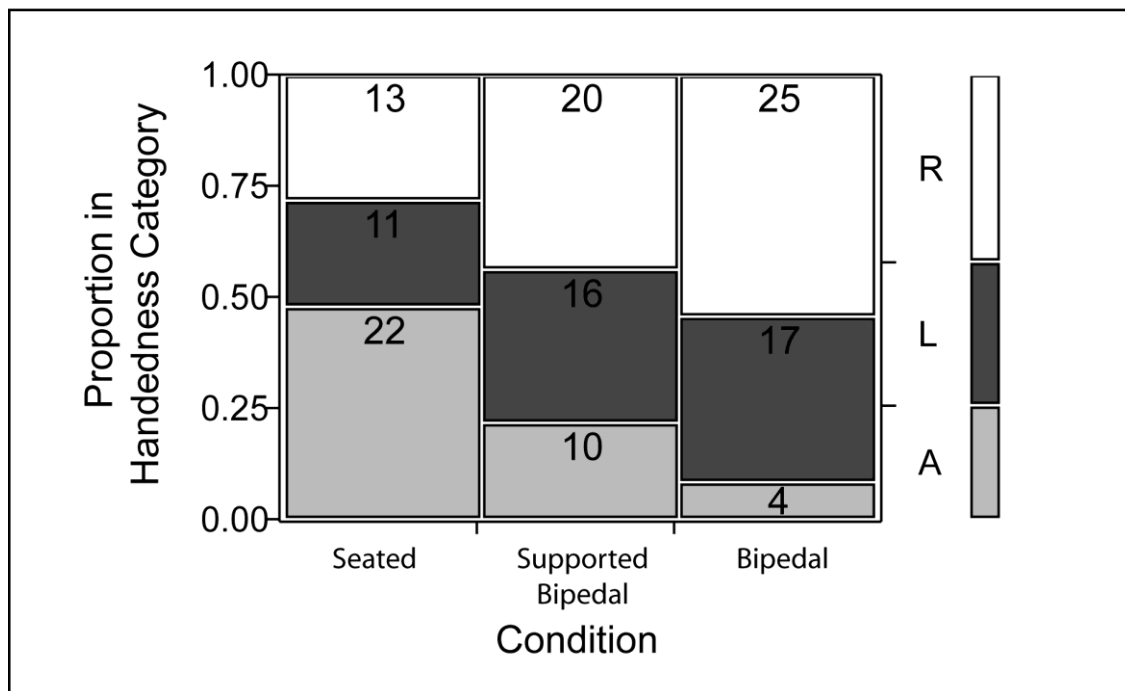
**Figure 2.3.** Mean absolute value of HI with error bars indicating mean standard error. The changes in mean absolute value of HI between the seated and the supported bipedal condition was significant ( $p < 0.02$ ), as was that between the supported bipedal condition and the unsupported bipedal condition ( $p < 0.01$ ), and between the seated and the unsupported bipedal posture ( $p < 0.001$ ).

### Categorized effects

Since the subjects used here were chosen based on their handedness category from a previous study conducted in 2002, the handedness results from that study were correlated with the results from the seated condition to ensure stability across time. The HI from the 2002 study is significantly correlated with the HI from the current seated condition,  $p < .01$ .

It is common in the literature to classify subjects as either left-handed, right-handed, or ambidextrous, based on the number of right- and left-hand responses. For comparison with other studies, subjects with a  $z$  score equal to or greater than 1.96 were considered right-handed, and subjects with a  $z$  score equal to or less than -1.96 were considered

left-handed (Figure 2.4). Subjects with  $z$  score values between these ( $-1.96 < z < 1.96$ ) were considered to be ambidextrous, reflecting the common practice used in the nonhuman primate literature (see Hopkins, 1999). The distributions of these handedness values differed significantly between conditions, when including all three postures (right-handed, left-handed, and ambidextrous) ( $\chi^2(4, N=138) = 19.599$ ,  $p < 0.001$ ), but when only the right-handed and left-handed categories are examined, the conditions no longer differ significantly ( $\chi^2(2, N=102) = 0.218$ ,  $p > 0.05$ ). As the task became more bipedal, the number of ambidextrous subjects dissolved into either right- or left-handed categories.



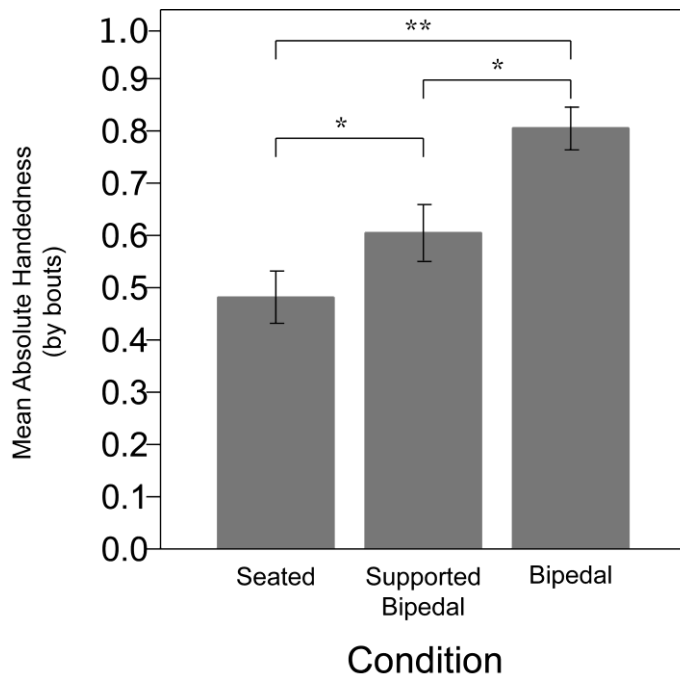
**Figure 2.4.** Number of right-handed, left-handed, and ambidextrous subjects by condition.

A repeated measures analysis of variance (ANOVA) was performed with experimental condition as the independent variable and HI as the dependent variable. No main effect was found ( $F [2, 44] = 0.762, p = 0.473$ ), suggesting that no preference was found for direction of preference. This was confirmed with a Wilcoxon signed rank test. The apparent increase in right-handedness and decrease in number of subjects showing no hand preference is not significant, but due to high variance.

### **Bouts *versus* Events**

To address potential confounds to the independence of the handedness measures (McGrew and Marchant, 1997), data were re-analyzed in terms of bouts (see Methods) and compared to the previous results. First, a strong significant correlation was found between HI (as measured with events) and HI using bouts ( $r = 0.714, p < 0.001$ ). The normality of the bout-oriented data was tested using the Kolmogorov-Smirnov goodness-of-fit test for both conditions 1 and 2 ( $p > 0.05$ ), but the bipedal condition showed a significant ( $p = 0.03$ ) departure from normality for both HI and AbsHI. Thus, a Wilcoxon matched-pairs signed ranks test was performed, comparing HI in the seated condition to the supported condition, the supported condition to the bipedal condition, and lastly, the seated condition to the bipedal condition. As before, absolute values of bout-wise HI differed significantly among conditions (seated to supported condition  $Z = -2.47, p = 0.013$ ; supported to bipedal condition  $Z = -3.80, p < 0.001$ ; seated to bipedal condition  $Z = -4.47, p < 0.001$ ) (Figure 2.5). Subjects increased their strength of hand preference as the task demanded more bipedality. However, as before, HI alone showed no significant change across conditions, showing no trend towards right- or left-handedness with increasing bipedality.





**Figure 2.5.** Mean absolute value of HI when re-examined per “bout” with error bars indicating mean standard error. The changes in mean absolute value of HI between the baseline and the supported condition was significant ( $p < 0.02$ ), as was that between the supported condition and the unsupported condition ( $p < 0.001$ ), and between the baseline and the unsupported bipedal posture ( $p < 0.001$ ).

## ***DISCUSSION***

This study is the first to include tool use in an examination of posture and hand preference in a large population of chimpanzees. The data show that during tool use in a bipedal posture, chimpanzee hand preferences become more lateralized to one side or the other. More specifically, as posture became less stable (from a seated to a supported bipedal stance to an unsupported bipedal posture) a significant increase in absolute handedness was observed. Subjects were most strongly lateralized when standing upright in an unsupported bipedal stance, compared to a supported bipedal stance or a seated posture, and were also more strongly lateralized when in the

supported bipedal stance compared to a seated posture. These data confirm those from the first hypothesis, that bipedal posture should increase lateral asymmetry, and thus the strength of hand preference toward either the right or left hand. However, a slight apparent bias towards being more right-handed as posture became bipedal was not significant, providing no support for the second hypothesis. This slight bias towards right-handedness may warrant further exploration, but my data do not support the suggestion that bipedal tool use drives most individuals towards right-handedness.

These findings have a number of implications regarding the evolution of laterality in humans, along with both theoretical and methodological implications for the study of laterality in other animals. We start by discussing the contribution of these data to current understanding of primate laterality in general, before turning to issues concerning human evolution.

### **Posture, Tool Use and Lateralization in Nonhuman Primates**

Various studies suggest that handedness in great apes may be linked to posture and/or tool use (Cantalupo et al., 2008; Hopkins, 1993; Hopkins et al., 2007; Olson et al., 1990). The effects of posture alone on hand preference have been previously examined in all four great ape species, and several studies report a right-hand bias when in bipedal versus quadrupedal posture. However, none of these studies directly examined bipedal tool use. The results of the current study differ from previous studies reporting that chimpanzees show significant population trends toward right-handedness for bipedal tasks (Hopkins and Morris, 1993). This disparity could be due to the differences in the methods employed. For example, these previous studies did not use a

seated posture as a baseline measure to preselect their subjects, nor did they examine tool use, or experimentally manipulate the degree of support.

From a methodological viewpoint, my results provide no support for the suggestion of McGrew and Marchant (1997) that bout-wise analyses provide a superior measure of hand preference, or that the findings of Hopkins et al. (2001), in a different population of chimpanzees, result from a statistical artifact of event-wise measures. With these individuals, and relatively large sample sizes, bout-wise and event-wise measures are very strongly correlated, so neither measure is clearly preferable.

To date, primate hand preferences have not been examined in light of species different morphology (Bradshaw and Rogers, 1993; Preuschoft, 1993), although grip morphology, in relation to hand preference, in chimpanzees has been explored (Hopkins et al., 2002). At the same time, in order to shed light on the evolution of handedness in early humans the morphology and skeletal asymmetry has been scrutinized (Cashmore, Uomini, and Chapelain, 2008; Lazenby, 2002). Some species differences may result from environmental or ecological factors (e.g. arboreality) that indirectly influence hand preference through posture. Primates such as bushbabies (Larson et al., 1989), ruffed lemurs (Forsythe et al., 1988), and gibbons (Olson et al., 1990) have exhibited non-population level left-hand preferences for bipedal food reaching (cf. MacNeilage et al., 1987). These species are more highly arboreal than chimpanzees, and perhaps require more visual spatial guidance, a function hypothesized to rely preferentially on the right hemisphere of the brain (Maravita and Iriki, 2004). However, bonobos also rely on arboreal locomotion more than

chimpanzees and appear to spend more time in trees, but show no consistent handedness (Doran 1993, D'Août, et al, 2004; Harrison and Nystrom, 2008). In gorillas, (Byrne and Byrne, 1991) found that while individual-level asymmetry in complex foraging tasks was often quite pronounced, no population-level bias existed. These gorilla results are thus quite similar to the experimental findings presented here.

The chimpanzees tested in this study became more lateralized (asymmetrical) as a result of experimentally induced changes in posture. As posture shifted from a familiar and relaxed seated posture to a less stable bipedal posture, the strength of hand preference increased as well. These results are congruent with those of Roney and King (1993) where cotton top tamarins and squirrel monkeys displayed higher levels of laterality while in a vertical clinging posture as compared to a quadrupedal posture.

Postural Origins Theory: After a long period of belief that no population-level laterality exists in primates, a seminal paper re-examined the data (MacNeilage et al. 1987), concluding that slight but significant preferences existed in many primates at the species level, which led to the "Postural Origins Theory" of human handedness (POT). The POT suggests that a basic lateralization to the left hand for grasping exists in many primates, leaving the right-hand to support the body in quadrupedal primates. With the assumption of upright bipedalism, the human right-hand was freed from this traditional role in support, and used to perform fine manipulations on the object grasped by the left hand. Thus, the human right-hand became specialized for tool use (MacNeilage, 1991).

The finding that posture has an effect on asymmetry lends partial support to the POT, which suggests that as primates became less arboreal, their postures shifted to reflect the most efficient feeding methods (MacNeilage et al., 1987). However, the research presented here does not support the further proposal of the postural origins theory that there should be an overall shift to a right-hand tool preference, for example due to the fine hand-eye precision required to insert a tool into a tube while standing bipedally.

Laterality, Arousal and Complexity: This study provides some support for the suggestion that hand preference may increase with arousal in the central nervous system (Larson et al., 1989; Westergaard et al., 1998), and for Fagot and Vauclair's (1991) theory that high-level, or difficult, tasks reflect specializations in the brain better than simple low-level tasks. The bipedal tool use task, especially without any support, was observed as being an uncomfortable and somewhat taxing task for the chimpanzee subjects in this study. The bipedal posture appeared for several reasons to be difficult for the chimpanzee subjects. Indicators of this difficulty include shaking legs during the task and resistance on the part of some animals to perform the bipedal task at all. Thus, the difficulty of maintaining a stable bipedal posture while performing a fine task may itself drive the chimpanzees to be more consistent in the hand they use to manipulate the tool in this task.

The task utilized here allowed me to separate the effects of difficulty, in general, from those arising from the specific complexity of tool use. Steele and Uomini (2009) correctly observe that discussions of "manual dominance" often forget that, in most tool making and tool use tasks, the left hand plays an important role in positioning or

stabilizing the target. Similarly, (Rogers, 2009) notes that discussions of "complexity" of tasks used in handedness research may ignore the fact that manual tasks may reflect the "processing styles" of the two cerebral hemispheres (e.g. for spatial relations versus fine detail), rather than complexity per se. Thus, human tool use is often better characterized by a division of labour among the hands, rather than simple "dominance" of one over the other. These criticisms, while often well founded, do not apply in this study. In the bipedal conditions, the non-tool using hand is only involved in postural stabilization and not in any aspect of tool use. Thus, this task cleanly separates the roles of difficulty from the complementary or synergistic use of the two hands, and shows that bipedalism drives increased laterality independent of any such synergy.

## **Implications for the Evolution of Human Handedness**

Discussions of the evolution of human handedness must cope with several seemingly contradictory observations. The first and most obvious is that humans show a degree of right-lateralization, roughly 90%, that is unparalleled in other primates (Gilbert and Wysocki, 1992; Perelle and Ehrman, 1994), especially in the context of tool use (Marchant et al. 1995; Stout 2002). Although debate about right-laterality in chimpanzees will continue, all parties agree that any population-level bias that exists in this species is not nearly as strong as in humans: roughly 65% whether for throwing, tool use, or gestural communication (Hopkins, 1996; Hopkins and Leavens 1998; Hopkins et al. 2005a). Furthermore, ambidextrality is common in chimpanzees but rare in humans (Hopkins, 2006). Field researchers have in general failed to find even this level of right bias in wild populations (McGrew and Marchant, 1997; Sugiyama et al., 1993), although Lonsdorf and Hopkins (2005) report a population-level bias for termite

fishing in wild chimpanzees. But any complete theory of handedness evolution will have to account for a major quantitative shift in right lateralization in the human lineage.

Despite the human species-typical right bias, a stable and significant number of humans are left lateralized, and the evidence available suggests that this polymorphism has existed for many tens of thousands of years (Coren and Porac, 1977; Llaurens et al., 2009; Steele and Uomini, 2005). This fact illustrates that left-handedness is perfectly compatible with successful existence as a human. More importantly, the persistence of left-handedness suggests that it has some advantage(s), apparently balancing the selection for right-handedness which might otherwise have driven humans to 100% right-handedness. While many hypotheses for this "balancing advantage" have been discussed (cf. Llaurens et al. 2009), the most likely seems to be an advantage enjoyed by left-handers in fighting and other physical competition (Annett, 1985; Ghirlanda et al., 2009; Porac and Coren, 1981).

Finally, cerebral asymmetry for language is even more pronounced than handedness. This is because, in addition to the 93% of right-handed humans left dominant for language (Knecht et al., 2000a; Knecht et al., 2000b), most left-handers are also left-dominant: only a small proportion (around 10% of 50 left-handed subjects) show true mirror-reversal and complete right hemisphere dominance (Pujol et al., 1999).

Cerebral asymmetry for language does not co-assort perfectly with handedness, and is both stronger than, and somewhat independent of, the motor asymmetry underlying handedness.

Cerebral asymmetry and handedness: While cerebral asymmetry was long argued to be a distinctive feature of humans (e.g., Annett, 1985; Corballis, 1983; Crow, 2004; Geschwind, 1970;) recent data overwhelmingly support the idea that cerebral asymmetry is widespread among diverse vertebrates for certain functions, notably communication and social behaviour (cf. Rogers, 2009; Rogers and Andrew, 2002; Vallortigara, 2006). This strong evidence contrasts sharply with the much weaker evidence for population-level handedness biases among nonhuman animals, and strongly suggests that handedness and cerebral lateralization for language, though often conflated, need to be clearly distinguished in discussions of the evolution of laterality.

The data presented here support the need for this distinction, and suggest a two-component (and perhaps two-stage) model of the evolution of human lateralization. First, my finding that the combination of tool use and bipedal posture drives chimpanzees to be more lateralized, but in a random direction, suggests that bipedal hominins from *Australopithecus* onward would have had more pronounced individual-level lateral asymmetries, at least during tool use, than those observed in modern chimpanzees. Many authors have proposed functional advantages to cerebral asymmetry in either direction, including the avoidance of unnecessary duplication of neural circuitry (Levy, 1977), and efficient parallel processing by the two hemispheres (Rogers, 2002). The data are clearly compatible with the idea that a strengthening of asymmetry would have occurred, and provided selective advantages, quite early in hominin evolution. Because basic tool use characterizes both chimpanzees and humans, and was thus presumably present in the last common ancestor of these species,



I hypothesize that a strengthening of individual asymmetry started as soon as early homnins assumed a habitual upright posture during tool use or foraging.

Language and Handedness: However, no evidence was found from chimpanzees that posture and tool use would be enough to drive population-level right bias beyond a level seen in modern great apes. This suggests that some additional factor must be invoked to explain the strong right bias found in all modern human populations. The most commonly-cited additional factor is language: what Steele and Uomini (2009) term the "Homo loquens" hypothesis. For example, Corballis has suggested that humans' extreme right bias for skilled action is better explained by lateralization for language than any specifically manual selective force (Corballis, 2003). By this hypothesis, population level right-handedness may represent an unselected by-product, or "spandrel" of left-brainedness, selected for independent functional reasons. This idea is supported by the fact, noted above, that language is in fact more lateralized than hand preferences because most left-handers are also left lateralized (Knecht et al., 2000b; Pujol et al., 1999). An alternative possibility is that language and manual specialization co-localize because both rely on some kind of "syntactic" or rule-governed process, and thus that lateralization based on tool-use preceded that for language (Bradshaw and Nettelton, 1982); the "Homo faber" hypothesis of Steele & Uomini (2009).

The data provide significant support for "language first" scenarios, although not for any sharp discontinuity in the evolution of handedness (e.g., Crow, 2004). My data clearly suggest that, although bipedality and tool may be enough to drive asymmetry in general

(e.g. in early bipedal hominids like *Australopithecus*), the specific localization of hand dominance to the right side, in all modern humans, appears to require some other force. Language lateralization appears to be a promising candidate.

Why should language drive a population-level bias? One factor may be ancient population-level brain asymmetries present in many vertebrates. Overwhelming evidence has now accumulated indicating that neural and behavioural asymmetries, particularly at the sensory level, are a ubiquitous feature in vertebrates (Vallortigara and Rogers, 2005). Although many species show asymmetry at the individual level (Bradshaw and Rodgers, 1993; Cowell et al., 1997; Tsai and Maurer, 1930), population-level laterality is well-documented in a much smaller number of vertebrates, including toads (Bisazza et al., 1996) and cockatoos (Rogers and Workman 1993; Rogers, 2007), and may be dependent upon sensory proclivities (Rogers, 2009). Although there is considerable variety in the species examined and means of perceptual testing employed, a general regularity seems to be that the left hemisphere is more involved in practice- or experience-dependent behaviours, while the right hemisphere specializes in instinctive as well as spatial tasks (Andrew and Rogers, 2002; Güntürkün et al., 2000). In particular, socially salient stimuli (e.g. recognition of conspecifics, or sexual behaviour) seem to be the preferential domain of the right hemisphere in many species. Thus biases for left-lateralization for social interaction, seen in many vertebrates, may have provided the seed for the evolution of pronounced human cerebral asymmetry for language. However, as already stressed, some other factor must be invoked to explain its extreme strength. One potential route for explaining the strengthening of a pre-existing left bias is group coordination. Ghirlanda and

colleagues have developed game-theoretic analyses showing that pressure for group coordination can lead to strong population-level biases in asymmetry (Ghirlanda and Vallortigara, 2004; Ghirlanda et al., 2009), and that such biases form an evolutionarily stable strategy against non-biased mutants. Because language use requires coordination among individuals in a social group, it is plausible that the evolution of language might require such a population-level bias. While the need for coordination does not itself explain a right- or left-bias, this additional selective pressure might have built upon the "seed" of pre-existing vertebrate sensory biases.

In summary, the data provide support for what Steele & Uomini (2009) term the "Homo loquens" model of the evolution of human asymmetry, whereby individual asymmetry was driven by bipedal posture and tool use, but population-level asymmetry was driven, probably much later, by the evolution of language. In this second stage, the need for group coordination might have provided the selective force, as suggested by Ghirlanda et al. (2009), and pre-existing vertebrate biases for social perception (Rogers, 2009) or weak primate biases for communication (Hopkins et al., 2005b) the "seed" that led to right bias becoming the default state for all modern humans. A contravening force favouring left-handedness for independent reasons such as fighting or other physical competition has maintained a low but significant level of left-handedness even since, in a stable polymorphism (Llaurens et al., 2009). This model integrates multiple existing models for the evolution of human handedness, and is consistent with theoretical models, data on human handedness and cerebral laterality, and the comparative data from both chimpanzees and a variety of other vertebrates. It

also supports the long-standing suggestion that archaeological evidence for handedness might be used to try to date the origins of language.

In their thorough review of fossil and material-culture evidence for right-handedness in hominin evolution, Steele and Uomini (2005) stress the tenuous nature of most of this evidence (Steele and Uomini, 2005). Although early paleoanthropologists claimed evidence for handedness in the genus *Australopithecus* (Dart, 1949), most recent commentators have rejected these suggestions, and associate the evidence for population-level handedness with the genus *Homo*, at the earliest (Steele and Uomini, 2005). Even in *Homo*, however, they found only a limited amount of evidence consistent with population-level right-hand bias until anatomically modern humans, with the data for Neanderthals providing the strongest evidence outside of our own species. In an influential study at the Koobi For one site, Toth (1985) found evidence for right-bias among flint knappers in Oldowan and Acheulean tool-making assemblages, but subsequent researchers have questioned the reliability of this archaeological signal (cf. Steele and Uomini, 2005). These data are also consistent with the two stage model sketched above, whereby strong individual-level asymmetries long preceded population-level hand preferences, later brought on by the evolution of language.

In conclusion, data from experimental work on handedness in chimpanzees can directly inform discussions of the evolution of human handedness. These data support the notion that the evolution of upright posture in early hominins could have had a direct and significant effect on levels of individual hand preference. Although the relatively

simple tool-use task in this study involved only one hand, and thus has the virtue of clearly separating the roles of posture and task difficulty from tool use per se, future studies might profitably investigate the role of posture on more complex tool use tasks that involve both hands. Such tasks might be more relevant to human hand preference, which typically involved synergy between the "dominant" and non-dominant hands. Although my data do not resolve the long-running debate concerning population-level hand preferences in chimpanzees, they underscore the widely recognized fact that any such preferences are quite weak in chimpanzees when compared to humans, and that they depend on the specific task chosen. The data presented here also clearly indicate that future studies need to pay careful attention to the posture assumed by primates when evaluating behavioural asymmetries, as posture can have a strong effect on the strength of asymmetries expressed. Finally, these results nicely illustrate the complexity of the possible interactions between basic hand preference, tool use, and bipedalism, and suggest that studies examining only one or two of these factors risk overlooking important patterns in the behavioural data.

## **CHAPTER 3: EYE PREFERENCE**

The data in this chapter are in a paper submitted for publication as:

**Braccini, S.,** Lambeth, S., Schapiro, S., and Fitch, W.T. Eye preferences in captive chimpanzees. *Animal Cognition*.

## **CHAPTER 3: EYE PREFERENCE**

### ***INTRODUCTION***

Structural and functional brain laterality were long believed to be unique characteristics of humans. However, research has shown that the brain lateralization extends out to other vertebrates (Vallortigara, Rogers, and Bisazza 1999), including birds (Vallortigara, Regolin and Pagni 1999), fish, reptiles, amphibians (Bisazza, Rogers, and Vallortigara 1998) and primates (Hopkins and Bard 1993), all exhibiting varying levels of laterality. There are two key expressions of brain laterality: motor laterality (asymmetry of movement and physical tasks) and perceptual laterality (asymmetries in viewing or eye use). Motor laterality has been extensively studied in a variety of species, most commonly through research on manual functions such as handedness. Perceptual laterality has mainly been examined in species with laterally placed eyes (Vallortigara et al. 2001) as it is related to the reception and transmission of sensory information to the central nervous system. Each hemisphere does not receive sensory information from a single stimulus in the same proportions because the contralateral optic fibers have a larger diameter and faster conduction speed than the ipsilateral optic fibers in most mammal species, especially apes (Watson and Hanbury 2007; Jeffery 2001). In essence, the contralateral hemisphere receives monocular visual information faster and of a different quality than the ipsilateral hemisphere (Bishop et al. 1953). Although, in some mammals uncrossed axons are intermingled with crossed axons while others remain segregated, this varies on a

species to species basis (Jeffery 2001). Because of this, eye dominance may indicate lateralization in the processing of visual information.

Eye preference has been recorded in humans with 66.76% of the research population displaying a right-eye preference for sighting tasks or the performance of monocular activities (Bourassa et al. 1996). Walls (1951) described various measures of eye preference from the very simple, requiring the subject to hold up one finger or look through a tube, to the more complex utilizing specialized optometric equipment. More importantly, one must distinguish between eye dominance (the tendency to prefer visual input from one eye over the other), sensory dominance (related to binocular rivalry where perception alternates between images presented to each eye), and acuity dominance (concerned with differences in visual sharpness).

Visual laterality has been reported in a number of species including birds, reptiles and primates (Chapelain and Blois-Heulin 2008; Vallortigara et al. 2001; Bisazza et al. 1998) dating back to 1938 when the first primate eye preference study was published reporting a right-eye preference for looking through a tube at a piece of food by three immature capuchin monkeys (Kounin 1938). Almost ten years later Cole (1957) reported a right-eye preference in seven adult pigtail macaques when viewing a food item through a tube. In contrast, a left-eye preference was found in a group of 19 immature rhesus macaques, and no preference was found for seven adult rhesus (Krupe, Boyle, and Patton 1966). More recently Rogers, Ward and Stafford (1994) measured eye preference in four adult female and two 1-month-old



bushbabies. All subjects displayed left-eye dominance for viewing both the researcher and food through a grid. This eye preference weakened when testing mother bushbabies as they viewed their babies being held by the tester, suggesting that arousal and/or the stimulus being viewed affected eye use. For red-capped mangabeys, the strength of eye preference has been correlated to food preference, implying a direction relationship (de Latude et al. 2009). Studies regarding the influence of a stimulus suggest that the direction of eye preference depends not only on the stimulus, but also on the subject's emotions towards it (Hook-Costigan and Rogers 1998).

Numerous studies have been published on various fish species that all report similar results; fish preferentially use the left-eye when presented with a familiar object or pattern and preferentially use the right-eye when viewing unfamiliar objects or patterns (Sovrano 2004; Sovrano et al. 2001; DeSanti et al. 2001; Sovrano et al. 1999; Bisazza et al. 1998). Several fish species also exhibit a left-eye preference for looking at their own image and a right-eye preference for inspecting a potential predator (DeSanti et al. 2001; Sovrano et al. 2001; Sovrano et al. 1999; Vanegas and Ito 1983). These data suggest an aspect of recognition or familiarity in the expression of eye preference, suggesting that lateralization is associated with species recognition, or recognition of familiarity. Similar to findings for primates, the lateral preference may also be related to the emotional valence of the object being viewed.

The 40 plus years of research on the hemispheric specialization of emotional processing has produced multiple theoretical models. Two of the more relevant theories to the study of eye preference are the “Valence Model” and the “Approach-Withdrawal” model. According to the Valence Model, the experience and expression of positive emotions are produced in the left hemisphere and negative emotions are processed and expressed through the right hemisphere (Davidson 1992; Ernhart et al. 1998). This model is based on multiple studies examining facial expressions and brain activity (via fMRI) while subjects observe emotional stimuli in order to assess patterns of hemispheric activation in various brain regions (Davidson et al. 1990). The Approach-Withdrawal model, which is not mutually exclusive with the valence model, states that the drives behind approach behaviours are primarily processed in the left hemisphere of the brain and those associated with withdrawal behaviours are processed in the right hemisphere (Demaree et al. 2005). Davidson and others have produced a variety of evidence over the past 10 years indicating the two hemispheres of the brain are differentially responsible for specific positive and negative emotions.

The aim of this study was to investigate eye preference in response to objects with varying degrees of relevance in captive chimpanzees. Similar data have not been previously published for any great ape species. The influence of each stimulus on both directional preferences and strength of eye use was examined, as were any shifts in eye preference. It was expected that the chimpanzee subjects would display a right-eye preference for viewing familiar and emotionally neutral objects, similar to the preference shown by humans (Bourassa, McManus and Bryden,

1996) and marmosets (Hook-Costigan and Rogers 1998). In addition, I hypothesized that eye preference would shift to either a weak left-eye preference or no preference when viewing threatening or unfamiliar objects.

## ***METHODS***

### **Subjects & Housing**

Looking behaviour by 45 adult chimpanzees (19 males and 26 females), ranging in age from 13 to 47 years (mean age of 28.8 years) was studied. The chimpanzee subjects were socially housed in groups of between four and 15 animals at the Michale E. Keeling Centre for Comparative Medicine and Research of The University of Texas MD Anderson Cancer Centre in Bastrop, Texas. All chimpanzees remained in their home enclosures (Primadomes® and open top corrals) for testing in all eight experimental conditions.

### **Apparatus**

Eye preference was tested using a monocular viewing box (50.8cm x 50.8cm) made from white Lexan® (polycarbonate resin thermoplastic) with a small viewing hole centered on the front panel (1.2cm in diameter). The purpose of the box was to force the subjects to view the test object using only one eye, while simultaneously concealing the object (Figure 3.1). The box was set on a plastic rolling cart at approximately standing eye level for the chimpanzee subjects (1.1 meter).



**Figure 3.1.** The monocular viewing device measuring 50.8cm x 50.8cm with a single 1.2cm viewing hole.

## Procedure

Each presentation began with separating the subject animal from the group; the subject was isolated in the indoor section of the enclosure while the remaining group members were in the outdoor enclosure to ensure eye preference was not dependent on, or influenced by, social cues. Out of view of the subject, the experimenter placed the stimulus object in the box and then rolled the cart into view of the subject, flush against the mesh caging. The cart was placed directly in front of the metal door separating the subject from group members outside, thus ensuring that eye preference was not directionally influenced by any noise coming from the door. The experimenter remained directly behind the device in order to keep an accurate spoken commentary on eye use and not to influence directional looking. Conditions were tested every weekday until all 45 chimpanzee subjects had seen all seven objects and the empty box. Objects were presented in random order and run on multiple individuals within a group on the same day, but only one 15-minute

trial was completed per animal per 24-hour period. At the end of each trial the animal was rewarded with a small slice of apple or 2 grapes, to ensure that the shifting process and trial were kept positive. The reward did not vary based on object presented and was only given once the viewing box was moved out of view. In the event that an animal did not approach the device the trial was rerun at a later time, but only when the experimenter was sure the subject was not able to view the object. A small web camera (Windows LifeCam VX-5000) was set up on top of the viewing box to record the eye used and the experimenter kept a spoken commentary on the subject's actions as well as the eye being used. We recorded data for all conditions from both video and the experimenter's commentary.

Eight conditions were tested, with each presentation of the box representing a single condition. One of seven objects was placed inside the viewing box at a time and each object was only presented once in order to preserve any pre-existing familiarity. An additional condition was tested where the box remained empty. Objects and related details are listed in Table 3.1. These objects reflect 3 categories based on emotional valence unique to this population of chimpanzees: food (a low quality food represented by biscuits versus a high quality food of bananas), novelty (the novel duck and canine face picture versus the commonly seen video camera), and fear or curiosity inducing (a mirror and a plastic rattlesnake). Snakes are present in the wooded and grassy areas around the chimpanzee enclosures at Bastrop, thus the animals are familiar with them and frequently fear bark when snakes are visible.

Condition	Emotional Valence	Object	Details
EMPTY	Low Arousal	None	Empty box presented
SNAKE	High Arousal, Fear Inducing	Plastic diamondback rattlesnake	114.3cm long
MIRROR	High Arousal	Pedestal mirror	Mirror positioned 15.5cm from hole for viewing reflection
BANANA	High Arousal, Food	Three whole bananas	Fresh yellow bananas used with little to no bruising
BISCUITS	Low Arousal, Food	3 Purina chow biscuits	Placed on a brown paper towel positioned to see all three biscuits
DOG	Low Arousal, Novel	Picture of a canine face	20.32 x 25.4cm picture of a light coloured golden retriever face
DUCK	Low Arousal, Novel	Rubber duck	Yellow, 8.25cm x 7.11cm
CAMERA	Low Arousal	Sony DCR-PC10 digital video camera	Black and silver, placed with LCD display closed, 20 x 6.35cm

**Table 3.1.** Test conditions with details on objects and emotional valence.

## Data collection and analysis

Individual subject eye preferences were determined based on an eye use index (EI).

Eye use indices for all animals were calculated to quantify the degree of lateral bias. This was done by subtracting the total number of left-eye uses (L) from the number of right-eye uses (R), and dividing by the total number of eye use instances (R + L):

$$EI = \frac{R - L}{(R + L)}$$

EI values range from 1.0 (extreme right-eye preference) to -1.0 (extreme left-eye preference). The absolute value of the eye use index (absEI) was also calculated

( $\text{absEI} = |\text{EI}|$ ); the absolute value of the EI score represents the strength of eye preference irrespective of direction and ranges from 0 (no eye preference) to 1.0 (extreme lateralization in one direction or the other). There was no minimum number of looks required for any condition. The term ‘look’ was used to designate one instance of looking (e.g., approaching and looking into the viewing box) and all events were incorporated as data points. ‘First looks’ were scored using only the first look after moving more than one body length away from the box and recorded as independent data points, consistent with bouts measures of hand use (McGrew and Marchant, 1997). The ‘initial look’ of each condition was also examined, being the first look of each trial. Each look was coded as -1 (left-eye) or 1 (right-eye). The number of looks ranged from 2 to 27 per subject per condition, while the number of first looks ranged from 2 to 13. Subjects with only one look were excluded from the analysis in order to ensure comparison between initial look and at least one subsequent look.

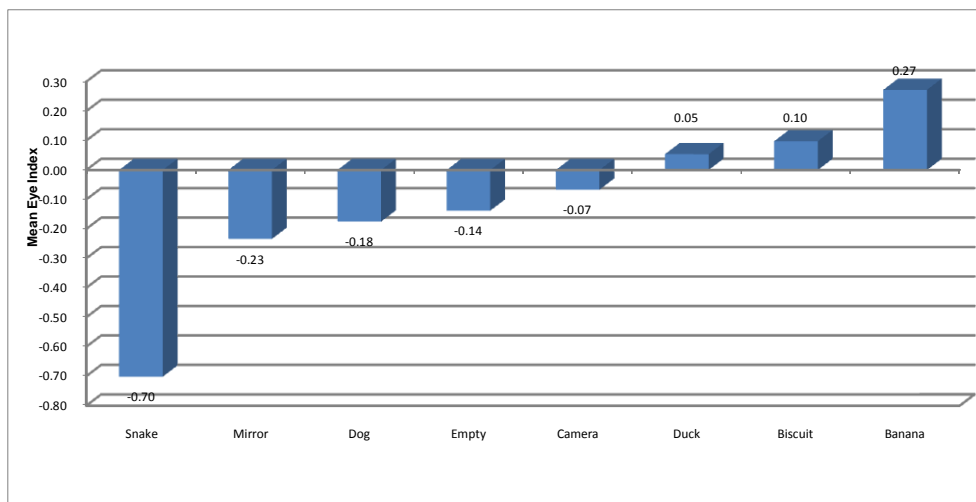
## ***RESULTS***

Significant deviations from chance were found for all looking measures (EI and  $\text{absEI}$ ) using a Kolmogorov-Smirnov test ( $p < 0.02$ ).

### **Direction of eye preference**

In order to evaluate the effect of stimulus on the direction of the eye preference, we examined the EI, as calculated using first looks, with a Friedman Test (Figure 3.2). The EI differed significantly across conditions ( $\chi^2=34.40$ ,  $p < .001$ ), with the snake

being viewed mostly with the left-eye (mean EI= -0.70) and the bananas being viewed mostly with the right-eye (EI= 0.27). The left-eye use for the snake condition was significantly greater than that for the mirror condition (Mann-Whitney U;  $Z=-3.29$ ,  $p=.001$ ), reflecting the strongest directional eye preference being shown for viewing the snake. These significant effects remained after adjusting for the number of analyses performed using a Bonferroni test.



**Figure 3.2.** Mean Eye Index per object presented (positive values reflect a right-eye bias while negative values reflect a left-eye bias). A significant difference in eye-preference was found across conditions ( $\chi^2 = 34.40$ ,  $p < .001$ ).

### Strength of eye preference

The absEI was also tested to determine differences in the strength of eye preference based on condition, but no significant effect was found ( $\chi^2=8.61$ ,  $p>.05$ ). This indicates that the only changes in eye preference, based on condition, were directional.



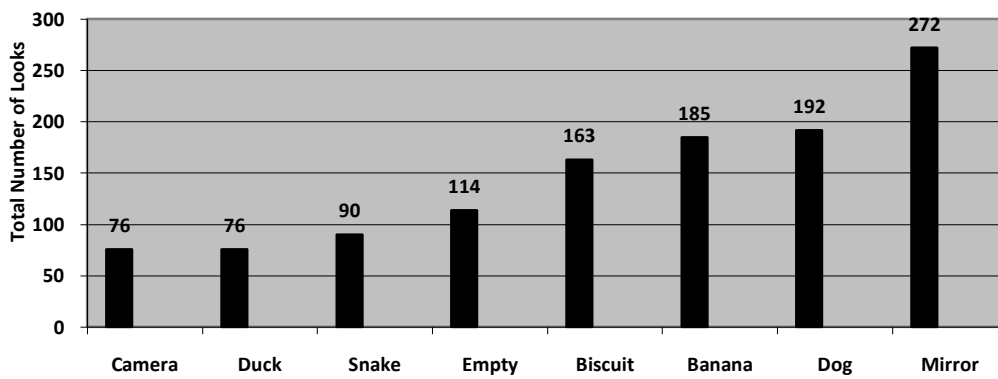
### **Initial look analysis**

In order to evaluate any change in eye preference within condition, the initial look was compared to the second look as well as the total eye use index. The only condition in which the eye preference changed from the initial look to the second, was the snake (Mann-Whitney U;  $Z=-2.83$ ,  $p=.005$ ). Eleven subjects initially looked with their right-eye while 27 used their left (for a mean EI of -0.42), but only two subjects took a second look with the right-eye (mean EI of -0.84). When comparing the initial look to the EI of each condition (reflecting overall eye use), only those for the bananas (Mann-Whitney U;  $Z=-2.029$ ,  $p=.042$ ) and snake ( $Z=-2.694$ ,  $p=.007$ ) were significant, even with a post hoc Bonferroni. In total, 30 of the 38 subjects who viewed the snake had negative EI scores reflecting a directional preference for left-eye use. The opposite was true for the banana where 33 of the total 45 subjects initially viewed the object with the right-eye (mean EI=0.47) then slowly began using the left-eye more often (mean EI=0.27). Across all first looks for the banana, 29 subjects had positive EI scores and 11 had negative. This reflects a shift away from right-eye use as looking progressed. By examining the initial look apart from subsequent looks I was able to determine which eye was used before the subject knew the contents of the box and then after, thus reflecting how the condition directly affected eye use.

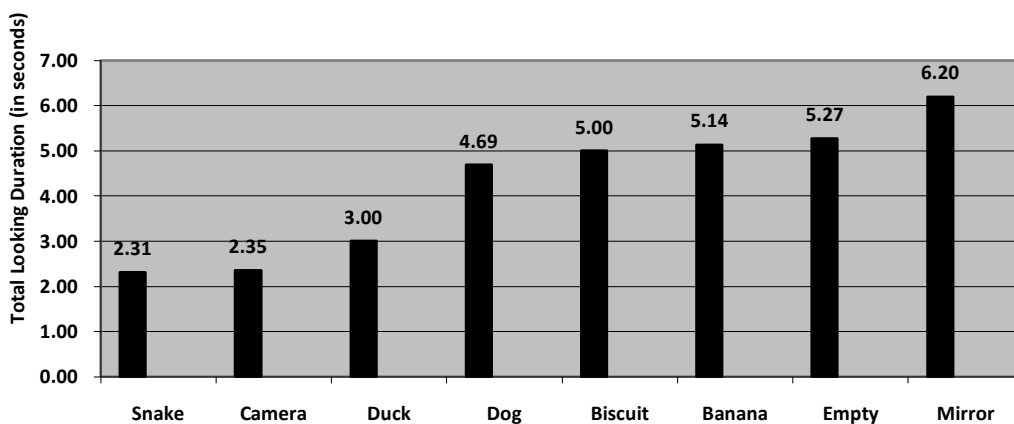
### **Number of first looks and viewing duration**

The number of first looks and viewing duration also differ significantly across conditions (Figures 3.3 and 3.4). Significant differences in the number of first looks across all subjects and conditions were found (Friedman test;  $\chi^2=74.32$ ,

$p < .001$ ), ranging from 76 (both camera and duck conditions) to 272 (mirror condition). Cumulative viewing duration varied significantly based on condition ( $\chi^2 = 74.86$ ,  $p < .001$ ), ranging from 6.2 seconds for viewing the mirror to 2.3 seconds for the snake.



**Figure 3.3.** Total number of looks per object presented. A significant difference in total number of looks was found across conditions ( $\chi^2 = 74.32$ ,  $p < .001$ ).



**Figure 3.4.** Total looking duration, in seconds, across all looks significantly differed between conditions ( $\chi^2 = 74.865$ ,  $p < .001$ ).

## **Categorical Analysis**

Analyses were also conducted based on categories of emotional valence (see Table 3.1): foods versus non-foods, low arousal versus high arousal, and novel versus familiar. The EI and AbsEI for each category were compared for significant differences in strength of eye preference and direction. It was found that the eye preference for viewing foods differed significantly from that for non-food items (Wilcoxon test:  $z = -2.39$ ,  $p = .017$ ). Food conditions were viewed more with the right-eye (mean EI=0.18) than non-food conditions (mean EI=-.21). Similar results were found for non-food high arousal conditions (snake and mirror), which were viewed significantly more with the left-eye than the right (Wilcoxon test:  $z = -3.77$ ,  $p < .001$ ). The mean EI for these conditions was -.45, while that of the remaining conditions was .02.

## **Eye use and handedness**

In order to fully examine laterality, EI and absEI scores were correlated with previously reported handedness measures for the same population (Braccini et al., 2010). Three handedness measures were tested; relaxed posture tool use, supported bipedal tool use, and unsupported bipedal tool use. The handedness indices (HI and absHI) for each posture were correlated with the eye use indices (EI and absEI) for each condition. The direction of eye preference (EI) did not significantly correlate with any of the handedness measures, but the strength of eye preference (absEI) did. The absEI values for the duck condition significantly correlated with handedness measures for both a supported bipedal posture ( $r = -.406$ ,  $p = .023$ ) and an unsupported bipedal condition ( $r = -.41$ ,  $p = .022$ ), but not for handedness while tool

using in a relaxed posture. In addition, eye use for the mirror condition correlated with handedness while tool using in an unsupported bipedal posture ( $r=-.328$ ,  $p=.028$ ). None of these effects were significant after applying a Bonferroni correction to avoid Type I errors.

### **Sex differences**

Collapsing across all conditions, no sex differences were found, with males exhibiting an average EI of 0.10 and females an average EI of -.10 (Mann-Whitney U;  $Z=-1.21$ ,  $p>.05$ ). In the empty box and mirror conditions, subtle significant sex differences were found. Females exhibited a stronger eye preference than males for the empty box (Mann-Whitney U;  $Z=-2.525$ ,  $p=.012$ ), with a mean EI of -0.18 for females and -0.08 for males. In the mirror condition females looked significantly more than males (Mann-Whitney U;  $Z=-2.022$ ,  $p=.043$ ), with females looking at the mirror 141 times and males 131 times.

### ***DISCUSSION***

This study, the first to examine eye preference in any great ape species, reports directional eye preference in response to various stimuli in captive chimpanzees. The results show (1) a difference from initial first eye use to subsequent eye use for both banana and snake conditions away from a right-eye preference (2) a group level bias for viewing the snake with the left-eye and the banana with the right-eye, and (3) significantly more and longer looks at the mirror than any other object.

Group level eye preference was reported for high quality food items, bananas, but not for any of the neutral stimuli (such as the empty box, biscuits, and video camera). These results are consistent with previous reports using low arousal stimuli with nonhuman primates (*Cercocebus torquatus torquatus*: de Latude 2009; *Callithrix jacchus*: Hook-Costigan and Rogers 1998; *Otolemur garnettii*: Rogers et al. 1994). The absence of significant laterality when viewing low or non-arousing stimuli could be due to the lack of emotional relevance related to the object.

Bananas are a known favourite food for the chimpanzees at the Keeling Centre, frequently eliciting food barks and visible excitement (hand slapping, bouncing, and play faces). During banana trials, eight food barks were recorded from various subjects upon the initial look at the bananas in the viewing box. The plastic rattlesnake also elicited vocalizations, with 12 instances of alarm calls or whimpering after the initial look. On three occasions, the subject looked to the experimenter for reassurance, either panting or reaching out, after the initial look. Since snakes are present at the Keeling Centre, these subjects were familiar with them and have been known to fear call in response to their presence (Braccini, personal observation).

Braccini and Caine (2009) have posited a connection between handedness, fear, and exploration in marmosets relating to both the Valence Model and the Approach-Withdrawal model. The Valence Model theorizes that the expression and experience of positive emotions are produced in the left hemisphere and negative emotions are processed and expressed through the right hemisphere (Davidson 1992; Ernhart et al. 1998). In the case of eye preference, the emotional valence of

the object may influence the eye used to view the object, but only after the subject knows what the object is, hence approaching and initially viewing an object with one eye, determining the emotional reaction to the object and then taking the second look with a different eye, as we report here. This could explain the adjustment in eye use from the initial look to subsequent looks for both the snake and banana conditions. These objects elicited the most emotional response of all the objects used and reflected both positive and negative extremes. The subjects could have previous knowledge or experience with a snake causing a negative emotional response (quantified with vocalizations indicative of fear). Bananas, being a preferred food item, also elicited an emotional response, but a positive one. The Approach-Withdrawal model theorizes that the drive behind approach behaviours are primarily processed in the left hemisphere of the brain and those associated with withdrawal behaviours from the right hemisphere (Demaree et al. 2005). If an object was repeatedly viewed, or viewed in long duration, one could theorize that it was not eliciting a negative emotional response worthy of withdrawal or retreat. The opposite would also be true, potentially explaining the shorter total viewing duration, fewer total looks, and significant left-eye preference for the snake condition; the subjects were actively avoiding looking at the snake, activating the right hemisphere. Since a change in eye preference was found from the initial look to subsequent looks for the two most emotionally valuable objects, the data presented here support both of these theories as emotional valence clearly played a role in eye preference.

For other nonhuman primates, emotion seems to play a distinct role in eye preference. Hook-Costigan and Rogers (1998) reported a right-eye preference in marmosets for viewing food or neutral stimuli and an absence of dominance or left preference for viewing negative stimuli. Rogers, Ward and Stafford (1994) studying small-eared bushbabies, theorized that eye choice is based on the nature of the visual stimulus. Eye preference shifted away from a left-eye preference when showing subjects their babies in comparison to a right-eye bias for viewing a novel stimulus. Both the novel object and the presentation of the baby increased arousal rates, potentially altering the eye preference exhibited.

In humans, eye dominance is associated with specialization of the contralateral hemisphere for language (Bryden 1988). In most individuals there is a left hemisphere specialization for language and right-eye dominance. Left-eye dominant individuals then make greater use of the right hemisphere and are found to show superior abilities to decode nonverbal cues (Domangue 1984). It has been reported that a majority of humans exhibit a right-eye preference for looking at neutral stimuli (Reiss and Reiss 1997). Since it has also been found that emotion is lateralized in the human brain (Davidson et al. 1990), the data presented here appear to be more in line with the human data than that presented for nonhuman primates.

Research in the past few decades has provided increasing evidence that brain lateralization may have appeared early in evolution, potentially beginning with perceptual processes (Rogers 2002; Vallortigara and Rogers 2005; Chapelain and

Blois-Heulin 2008). Given the recent data indicating cerebral lateralization in a wide variety of vertebrate species, it is very likely that some basic laterality was present in our ancestors long before the evolution of language, or of dexterous human hands used for making tools (Bisazza, Rogers, and Vallortigara 1998). This contradicts some established theories regarding the evolution of human brain lateralization, language and hand use (McGrew and Marchant 1997). With evidence of brain lateralization for perceptual functions in low vertebrates (Vallortigara 2000) it is suggested that hemispheric specialization may have evolved from eye preference, or perceptual laterality, and then influenced manual laterality; although it is always possible that both evolved independently.

This study revealed a preference in eye use for captive chimpanzees at the group level. These preferences were found only for the two most emotionally relevant objects, a rubber snake and a bunch of bananas, supporting the valence theory of hemispheric specialization of emotions (Davidson 1992; Ernhan et al. 1998).



## **CHAPTER 4: INDIVIDUAL PREFERENCES FOR AUDITORY LATERALITY**

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### ***INTRODUCTION***

Support for a left hemisphere dominance of language processing in humans has been clearly established over the past century (Belin et al., 1998; Bethmann et al., 2007; Fischer et al., 2009; Geschwind, 1970; Geschwind and Levitsky, 1968) suggesting that the left cerebral hemisphere of the human brain is more involved than the right in both the production and perception of speech sounds (Petersen et al., 1978). Humans show significant left hemispheric biases for both signed and spoken language and a right hemisphere dominance for producing and interpreting facial expression (Bradshaw and Rogers, 1993; Corballis, 1991). There are several indications that other factors may also affect lateralized auditory processing such as communicative significance (Yasin, 2007), emotional valence (Basile, Lernasson, and Blois-Heulin, 2009), and the source being a conspecific or heterospecific (Hauser and Andersson, 1994; Teufel, Ghazanfar and Fischer, 2010).

It's long been thought that humans were unique in showing brain lateralization (e.g. Geschwind, 1970) studies with non-human primates and other animal species have challenged the idea that lateralized processing of conspecific communication is unique to humans. Studies argue that rhesus macaques (Ghazanfar, Smith-Rohrberg, and Hauser, 2001; Hauser and Andersson, 1994; Hauser, Agnetta, and Perez, 1998), Japanese macaques (Beecher et al., 1979; Petersen et al., 1978), and sea lions (Böye, Güntürkün and Vauclair, 2005) all show varying degrees of left

hemisphere dominance. A few exceptions have been noted with vervet monkeys (Gil-da-Costa and Hauser, 2006) and Barbary macaques (Teufel, Hammerschmidt, and Fischer, 2007) suggesting that auditory laterality of conspecific communication may be affected by various factors. First is emotional valence; stimuli that elicit a negative emotional result are reported to be processed preferentially by the right hemisphere in dogs (Siniscalchi, Quaranta, and Rogers, 2008) and Campbell's monkeys (Basile, Lemasson, and Blois-Heulin, 2009). In contrast, adult male mouse lemurs display a left hemisphere dominance for processing sounds with negative emotional content (Scheumann & Zimmermann, 2008). Second, communicative significance has been reported to affect laterality in Japanese macaques, with a left hemisphere preference being shown for familiar and "meaningful" calls (Petersen, et al., 1978; Petersen, et al., 1984). Basile, Lemasson, and Blois-Heulin (2009) compared Campbell's monkeys to human 8- and 9-year old girls where a right turn bias was found in response to a negative context vocalization produced from a non-familiar conspecific, but no bias was reported for positive valence vocalizations. Campbell's monkeys also failed to exhibit any bias towards positive vocalizations, yet did display a left bias for species-specific negative vocalizations.

Third, the source of the vocalizations has been theorized to alter laterality, depending on whether the sound was produced by a heterospecific versus conspecific. In a study with Barbary macaques two different species specific calls and three different heterospecific calls were used and no significant orienting difference was found (Teufel et al., 2007). Mouse lemurs also failed to show any

asymmetry to three difference conspecific calls or to seven heterospecific calls (Scheumann and Zimmermann, 2008). Yet, in a study with vervet monkeys, a left turning bias was reported for species-specific vocalizations while no bias was present for heterospecific or non-biological sounds (Gil-da-Costa and Hauser, 2006). Lemasson et al (2010) reported similar findings for Japanese macaques, where a left turn bias was reported in response to species-specific calls but not for non-biological sounds. Additional studies on non-primate species further highlight the lack of consistency in orienting responses. Dogs (Siniscalichi et al., 2008), California sea lions (Böye et al., 2005) and domestic horses (Basile, Boivin, et al., 2009) all exhibited a right turn bias only for conspecific vocalizations.

The orienting literature also documents inconsistent results regarding human orienting behaviours. Fischer et al. (2009) report no difference in orienting asymmetries in relation to human speech or artificial sounds, while an fMRI investigation confirmed that the speech condition evoked a significant left lateralized activation compared to the artificial sounds. This was the first publication to directly compare behavioural laterality (turning bias) to neural responses.

A possible non-invasive indicator of auditory laterality in animals is the head turn paradigm reported by Hauser and Andersson (1994) for rhesus macaques. This simple assay requires that an auditory cue be broadcast from behind a subject, and then the side to which the subject rotates or looks is recorded. The key assumption is that since both ears receive the same auditory cue, turning to one side intensifies

the input and potentially creates a bias to that contralateral hemisphere. However Teufel et al (2010) argue persuasively that several of the assumptions underlying this assay are invalid.

This study aims to examine orienting asymmetries to conspecific and heterospecific vocalizations by replicating the methods of Hauser and Andersson's (1994) macaque study with captive chimpanzees.

## ***METHODS***

### **Subjects & Housing**

The 30 (14 male and 16 female) chimpanzee subjects used in this experiment were housed at the Michale E. Keeling Centre for Comparative Medicine and Research, Department of Veterinary Sciences, University of Texas M.D. Anderson Cancer Centre in Bastrop, Texas ('Bastrop'). In addition to open top corrals, the facility has 15 occupied Prima-domes©, each providing both indoor and outdoor housing. Each dome houses between three and six animals and all of these dome populations were used for this study.

### **Materials**

In order to best replicate the methodology used by Hauser and Andersson (1994) a EBP-6000 Explorer Pro speaker was set up 180° behind the subject, concealed in an excelsior covered box which resembled a bale of excelsior (a common bedding

material with which the animals were familiar). The concealed speaker was placed on a wagon to facilitate movement and camouflage the speaker from the chimpanzees. Similar carts and wagons were used throughout the facility on a regular basis.

All trials were recorded on a Panasonic SDR-S15 digital video camera. Two types of calls were used; unfamiliar conspecific vocalizations (food calls provided by Michael L. Wilson and recorded at Kanyawara Research Centre, at Kibale National Park in Uganda) and unfamiliar heterospecific vocalizations (American crow calls, recorded in Central Texas, provided by Cornell Lab of Ornithology Macaulay Library). Crows are a common species at Bastrop, and this class of calls was frequently heard at my study site. Four calls of each type were used to reduce issues of pseudo-replication, and one call from each of these classes was played to each chimpanzee subject (two playbacks total, per animal).

## **Procedure**

The speaker was placed 180° behind and approximately 4 meters away from the subject, facing the experimenter, as in Hauser and Andersson (1994). All playback trials were video recorded and later coded for the first exhibited direction of head turning greater than approximately 45 degrees from the pre-playback position. All behaviours exhibited within the first 3 minutes (head turning, body turning, body orientation, vocalizations, and any directional movement) were also coded. Playbacks were conducted from an Apple MacBook laptop computer with signal output through a single speaker. All calls were played at the same volume and calls

were compared to ensure similar length, clarity, and amplitude. Each subject was tested with one call per day, with a minimum of 24 hours between trials. The order of stimulus presentation was randomized.

Since this study tested captive animals, trials began when all members of a group were confined to the indoor section of their enclosure. While the animals were indoors, the speaker and camera were set up. Once the equipment was in place, one focal animal was called outside and locked into the outdoor section of the enclosure. In three cases the subject was hesitant to be locked out alone, so two additional non-subject group members were locked out as well. In these three cases, the non-subject group members were seated to either side of the subject to balance out any influence they may have on directional head turning. Subjects were given juice for their cooperation upon entry into the enclosure and then their attention was focused on the experimenter who provided grapes to the subject. In Hauser and Andersson (1994) the speaker was set up directly behind a food dispenser, so the use of food to direct attention is consistent with that methodology. As soon as the chimpanzee subject was oriented directly across from the speaker, and looking away from it, one of the eight calls was played. Responses were coded from video and defined as the first distinctive ( $>45^\circ$ ) head turn, in either the right or left direction, along with any other behaviours exhibited within the first 3 minutes. After 5 minutes the subject and any other animals were returned to their indoor enclosure and the equipment was removed. Finally, the group was given renewed access to their outdoor habitat.

In order to maintain novelty of the auditory stimuli, neighbouring chimpanzee groups were sequestered to their indoor enclosures during trials, ensuring they could not hear the playbacks.

## **Data Collection and Analysis**

Head turning indices (HTI) across all subjects were calculated in order to quantify the degree of head turning bias. This was performed by subtracting the number of turns to the left (L) from the number of turns to the right (R), and dividing by the total number of head turns (R + L):

$$HTI = (R - L) / (R + L)$$

Head turning indices range from 1.0 (extreme right bias) to -1.0 (extreme left bias). Absolute Head Turning (absHTI) was also calculated and represented the strength of the bias regardless of direction ranging from 0 (no bias) to 1.0 (extreme bias). Statistical analysis was performed using SPSS version 16 software.

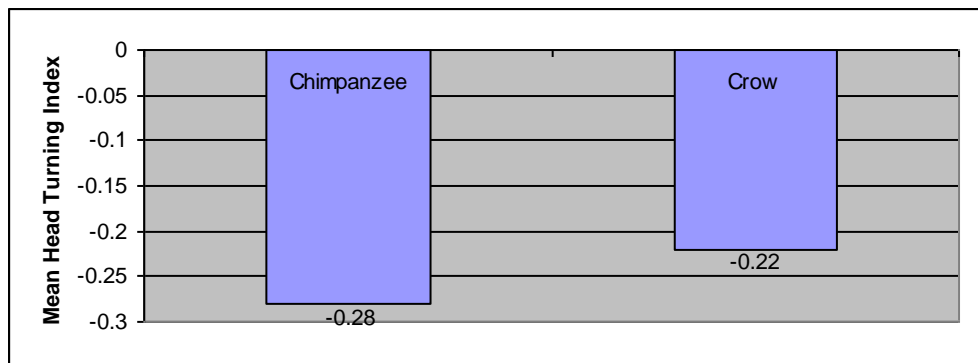
## ***RESULTS***

No significant deviation from normality was found (Kolmogorov-Smirnoff test,  $p > 0.05$  for both conditions), for both Head Turning Index (HTI) and the absolute Head Turning (absHTI). Therefore, parametric statistics were used for analysis.

To best examine the effect of call type on head turning laterality, we compared HTI and absHTI for both call types. Mean HTI for the chimpanzee calls was -0.28, and



-0.22 for the crow calls (Figure 4.1) thus subjects showed an overall left bias for all calls. A repeated measures t-test compared HTI for the chimpanzee and the crow call, and showed no significant difference ( $t(27) = -0.75, p=.46$ ). To test for significant differences in strength of head turning, regardless of direction, the absolute value HTI was analyzed and also failed to yield any significant difference ( $t(27) = 0.414, p=.68$ ). Informal analysis of the other recorded behaviours failed to reveal other patterns of responses that differed between the two call categories.



**Figure 4.1.** Mean Head Turning Indices for both the chimpanzee calls and the crow calls ( $t(27) = -0.75, n.s.$ ).

### Individual eye preferences

An overall turning bias towards the left was seen for both conditions. Responses to the chimpanzee calls were significantly consistent to the left ( $t(27) = -2.8, p=.009$ ), while responses to the crow calls were not significant ( $t(27) = -1.9, p=.067$ ). All but four subjects were consistent in their left turning direction, regardless of call type played (three subjects turned to the left for the chimpanzee vocalization and then switched to a right bias for the crow and only one went from right to left.)

## ***DISCUSSION***

The experiments conducted here constitute a replication of Hauser and Andersson's (1994) study with macaques. The chimpanzee subjects used here showed a significant left bias for all call types, but failed to produce any differential head turning bias for processing conspecific vocalizations relative to heterospecific crow calls; failing to replicate the result reported in Hauser and Andersson (1994). These results are in contrast to several highly-publicized studies in both nonhuman primates and other animal species, but are consistent with recent results from Fischer et al 2009 for human subjects. Fischer et al. 2009 reported no difference in orienting asymmetries in relation to the stimulus material played, rather human subjects exhibited a significant left bias regardless whether the auditory stimulus was human speech or an artificial sound.

Humans are the ideal test subject for testing orienting asymmetries since the lateralized processing of speech is already clearly established (Geschwind, 1970; Geschwind and Levitsky, 1968). Fischer et al. (2009) examined the link between orienting asymmetries and hemispheric lateralization in the processing of sounds in adult humans by comparing the results from a naturalistic behavioural orienting experiment (using speech and artificial sounds) to those from an fMRI study of brain activation listening to the same sounds. As expected, the left Broca's area and frontal operculum showed higher activation for the human speech condition than for the artificial sound. Combined, their results suggest that the well-known lateralized processing of speech versus other stimuli does not lead to concordant orienting biases. These behavioural results are more in line with the human

literature than that of the (quite inconsistent) primate literature: a generalized left bias and no difference for conspecific (speech) and heterospecific (or artificial) sounds.

Specializations for processing speech in the left hemisphere are well established in humans (e.g., Basile, Lemasson, & Blois-Heulin, 2009; Fischer et al., 2009; Geschwind 1970), but studies regarding non-human specializations are far more variable. Previous literature reports California sea lions (Böye, Güntürkün, & Vauclair, 2005) and mice (Ehret, 1987) as displaying a left hemisphere dominance, while vervet monkeys (Gil-da-Costa & Hauser, 2006), Campbell's monkeys (Basile, Lemasson, & Blois-Heulin, 2009), and rhesus macaques (Hauser, Agnetta, & Perez, 1998) have all shown a right hemisphere preference. In contrast, Teufel, Hammerschmidt, and Fischer (2007) failed to find orienting asymmetry in Barbary macaques in response to playbacks of both conspecific and heterospecific vocalizations using the same Hauser head turning paradigm.

The inconsistencies in the considerable literature on auditory lateralization as measured by head turning all have one thing in common: the basic orienting asymmetry paradigm. This methodology, due to Hauser and Andersson (1994), has attracted considerable attention, replication and skepticism over the years. Teufel, Ghazanfar, and Fischer (2010) present a strong critique of the implicit assumptions of the orienting asymmetry paradigm and conclude that serious caution is warranted when interpreting results utilizing this paradigm. In Japanese macaques the head turning paradigm resulted in a left turn (right hemisphere) bias in response to

conspecific calls (Lemasson et al., 2010), yet this same species has repeatedly been used in neurobiological research displaying a left hemispheric specialization of processing conspecific sounds (Heffner and Heffner, 1984; Petersen et al., 1978). Similar results have been presented for work with rhesus macaques; PET studies presenting a right neural lateralization for conspecific calls (Gil-da-Costa et al., 2006) while orienting asymmetry experiments report a left hemisphere dominance (Hauser and Andersson, 1994). Fischer et al. (2009) performed behavioural and fMRI studies on the same human population and failed to find any significant correspondence between head turn direction and brain activation, leading them to argue that the behavioural response does not accurately reflect the brain activation. Instead the authors reported an overall left bias for the orienting behaviour, irrespective of the sound category (speech or artificial sound) and a left lateralized brain activation, suggesting that in adult humans the orienting biases are not necessarily reflective of lateralized processing. Without neurological studies on all species to correspond with behavioural observations, there can be no clear resolution to the question of whether orienting asymmetries can be accepted as evidence of underlying cerebral asymmetry.

In addition to the numerous inconsistencies between behavioural and neurological data, small sample sizes plague most research using this paradigm, and the literature potentially suffers from publication bias for positive results. More broadly, we lack any substantial theory on which to base the assumption that lateralized auditory processing is directly translated into a turning bias. All of these studies are based on the single assumption that one hemisphere is activated during

the processing of an acoustic stimulus and that activation leads to a visually guided physical movement towards the contralateral side. But other mechanisms could also be at work, such as motor control of the neck muscles. Hopkins and Fernández Carriba (2002) argue that the neck muscles responsible for the orienting are controlled by a ventromedial neural pathway, which projects ipsilaterally in the brain, so the orienting response to the right would mean activation of the right hemisphere and not the left as presumed in Hauser and Andersson (1994). The action of eating during the playbacks has also been theorized to affect orienting bias, as reported in humans (Milberg et al., 1981). Movements of the articulatory system (jaw, tongue, lips, etc.) may activate the left hemisphere as they normally accompany speech, which would result in a right turn bias unrelated to the playback stimulus. Although it does not explain the left turn bias reported by Hauser and Andersson (1994) or the results reported here, it does contribute additional grounds for caution when interpreting the inconsistent data on orienting asymmetries stemming from the use of the head turn paradigm.

In conclusion, these results fail to support the hypothesis that chimpanzees exhibit different or significant orienting asymmetries in response to conspecific vocalizations and heterospecific vocalizations. These results, while congruent with the recent human data for an overall left bias regardless of stimulus, are contradictory to some of the literature for other primates, and other mammal species. These results provide support for a growing skepticism about the value of head turning as an assay for neural lateralization. These results present a methodological replication of Hauser and Andersson (1994), but fail to replicate

their findings in chimpanzees, and in combination with previous literature, we stress the need for skepticism and considerable caution before any firm conclusions about the evolutionary and neural bases for cerebral lateralization can be drawn.

## **CHAPTER 5: GENERAL DISCUSSION**

## **CHAPTER 5: GENERAL DISCUSSION**

The objective of the work within this thesis was to contribute to current scientific understanding of the behavioural expressions of hemispheric asymmetry and laterality in great apes. In humans it is believed that lateralized behaviours (handedness, eye preference and head turning) are related to brain lateralization of language and other cognitive functions. Since lateralized behaviours are not unique to humans they have recently become a popular topic of research, especially when attempting to trace the origins of laterality from the common ancestor of great apes to humans.

### ***Overview of experiments***

#### **Chapter 2: Chimpanzee Handedness, Tool Use, and Bipedalism**

The study presented in Chapter 2 of this thesis was the first to include tool use in an investigation of posture and hand preference in a large population of chimpanzees, and remains the only study to do so. This study examined the relationship between hand preference and posture during a tool use task by manipulating the task demands so that tool use could be performed while seated, while bipedal with one hand against a wall, and while fully bipedal. It was hypothesized that the bipedal posture would increase the strength of hand preference, regardless of direction, and that the bipedal posture would encourage a right-hand preference. While in a bipedal posture, chimpanzee hand preferences did become more lateralized, but not in a universal direction. As posture became less stable (from a seated to a



supported bipedal stance to an unsupported bipedal posture) a significant increase in absolute handedness was observed, reflecting the strength of hand preference regardless of direction. The results this confirmed my first hypothesis, that bipedal posture would increase lateral asymmetry, and thus the strength of hand preference toward either the right- or left-hand. However, a slight bias towards being more right-handed as posture became bipedal was not significant, failing to support the second hypothesis.

Data from empirical research on handedness in chimpanzees can directly impact discussions of the evolution of human handedness. The results presented in Chapter 2 support the notion that the evolution of upright posture in early hominins could have had a direct and significant effect on levels of individual hand preference. The relatively simple tool use task in this study involved only one hand, and thus has the virtue of clearly separating the roles of posture and task difficulty from tool use. While my data do not resolve the long-running debate concerning population level hand preferences in chimpanzees, they underscore the widely recognized fact that any such preferences are quite weak in chimpanzees as compared to humans, and that they depend on the specific task chosen. This data also clearly indicate that future studies need to pay careful attention to the posture assumed by primates when evaluating behavioural asymmetries, since we showed that posture can have a strong effect on the strength of any asymmetries expressed. These results nicely illustrate the complexity of the possible interactions between basic hand preference, tool use, and bipedalism, suggesting that studies examining

only one or two of these factors risk overlooking important patterns in the behavioural data.

Chapter 2 reported a significant relationship between posture and handedness, highlighting a potential pre-existing lateral bias, to either the right or left, which increased as postural demands became more taxing. The subsequent chapters of this thesis aimed to investigate additional lateralized behaviours in the same population of chimpanzees.

### **Chapter 3: Chimpanzee Eye Preferences**

Over the last century, the issue of brain lateralization in primates has been extensively researched and debated, but surprisingly no previous study has investigated eye preference in great apes. Chapter 3 examined eye preference in the same population of captive chimpanzees in response to various stimuli. Eye preference was assessed when animals looked through a hole that would only accommodate one eye into an empty box, or at a mirror, a picture of a dog, a rubber snake, food biscuits, bananas, a rubber duck or a video camera. It was hypothesized that the chimpanzee subjects would display a right-eye preference for viewing familiar and emotionally neutral objects, similar to effects reported in humans (Bourassa, McManus and Bryden, 1996) and marmosets (Hook-Costigan and Rogers 1998). In addition, I hypothesized that eye preference would shift to either a weak left-eye preference or no preference when viewing threatening or unfamiliar objects.

The results showed that eye preference, number of looks and looking duration all varied depending on the object inside the box. A left-eye bias was found for viewing a realistic rubber snake (a dangerous and arousing stimulus) and a right-eye bias was found for viewing the bananas (high quality food), supporting my first hypothesis. In addition, a significant shift in eye preference was reported from the initial look to subsequent looks when viewing the snake, indicating that the eye preference changed in response to the presence of the snake. These results are not consistent with previous reports of human eye preference and may reflect lateralization differences for emotional processing since the most significant results are those in response to a high value food item and a fear inducing snake.

Chapter 3 revealed a preference in eye use for captive chimpanzees at the group level, but only for the two most emotionally relevant objects, a rubber snake and a bunch of bananas. These preferences support the valence theory of hemispheric specialization of emotions (Davidson 1992; Ernhart et al. 1998). According to this theory, the experience and expression of positive emotions are produced in the left hemisphere and negative emotions are processed and expressed through the right hemisphere (Davidson 1992; Ernhart et al. 1998). This model is based on multiple studies examining human facial expressions and brain activity (via fMRI) while subjects observe emotional stimuli in order to assess patterns of hemispheric activation in various brain regions (Davidson et al. 1990). Given the strong responses seen for the emotionally significant objects it can be tentatively concluded that emotional significance influences eye preference in chimpanzees. The role of emotion is discussed further at the end of this chapter.

## **Chapter 4: Orienting Asymmetries in Chimpanzees**

Chapter 4 presents another study that was the first of its kind to be conducted with chimpanzees, a replication of Hauser and Andersson's (1994) examination of orienting asymmetries in rhesus macaques, in response to conspecific and heterospecific vocalizations. A different study group of chimpanzees was utilized for Chapter 4, housed at the same facility. The methodology requires that an auditory cue be broadcast from behind a subject, and then the side to which the subject rotates or looks is recorded. The key assumption underlying much research on orienting asymmetries is that, since both ears receive the same auditory cue, turning to one side intensifies the input and potentially creates a bias for processing further input in the contralateral hemisphere. While this assumption may be correct under some circumstances, Teufel et al (2010) argue persuasively that several of the assumptions underlying this assay are invalid.

The results in Chapter 4 suggested a slight left bias for all call types, but failed to produce any significant head turning bias for processing conspecific vocalizations or heterospecific crow calls; failing to replicate the same pattern of results as reported in Hauser and Andersson (1994). These results are in contrast to several highly-publicized studies in both nonhuman primates and other animal species, but similar to the results of human research by Fischer et al (2009). Fischer et al. (2009) failed to find any significant difference in orienting asymmetries in relation to the stimulus material played, rather human subjects exhibited a significant left bias regardless of whether the auditory stimulus was speech or an artificial sound, similar to what my research, reported in Chapter 4, found.

As indicated in the Introduction to this thesis, the results of the many studies examining animal auditory laterality are inconsistent across, and sometimes within, species. The inconsistencies across this large literature all have one thing in common: the basic orienting asymmetry paradigm. This methodology has attracted considerable amounts of attention, replication and skepticism; the most critical being Teufel (2010) who present a strong critique of the implicit assumptions of the orienting asymmetry paradigm. Teufel and colleagues conclude that serious caution is warranted when interpreting results from this paradigm. For example, in Japanese macaques, the head turning paradigm elicited a left turn (putative right hemisphere) bias in response to conspecific calls (Lemasson et al., 2010), yet this same species has repeatedly been used in neurobiological research as displaying a *left* hemispheric specialization for processing conspecific sounds (Heffner and Heffner, 1984; Petersen et al., 1978). PET studies with rhesus macaques report a right neural lateralization for conspecific calls (Gil-da-Costa et al., 2006) while orienting asymmetry experiments suggest a left hemisphere dominance (Hauser and Andersson, 1994). Fischer et al. (2009) performed a behavioural and fMRI study with adult humans and failed to find any significant correspondence between head turn direction and brain activation, leading them to argue that the behavioural response does not accurately reflect brain activation. Instead an overall left bias for orienting behaviours was reported, irrespective of the sound category (speech or artificial sound) and left lateralized brain activation, suggesting that orienting biases are not necessarily reflective of lateralized processing.

Given the amount of critique surrounding the basic methodology, I interpret the results of my own study quite cautiously. The results from Chapter 4 fail to support the hypothesis that chimpanzees exhibit significant orienting asymmetries in response to conspecific vocalizations and heterospecific vocalizations. The results are an attempt at replication in a different species, of Hauser and Andersson's (1994) result, and in combination with previous literature, this negative result underscores the need for skepticism and considerable caution before any firm conclusions about auditory lateralization can be reached using this methodology.

## ***Conclusions***

### **Role of emotion / arousal**

While the existence of brain lateralization among vertebrates has only recently been widely accepted (Rogers and Andrew, 2002; Vallortigara and Rogers, 2005), the link between hemispheric asymmetry and emotional processing continues to be debated (Campbell, 1982). Early reports suggested that the emotional content of language is processed in the right hemisphere (Heilman et al., 1975) and that the right hemisphere is more involved in the processing of negative emotions, linking the left hemisphere with approach behaviours and the right hemisphere to avoidance behaviours (Davidson, 1992; Hopkins and Bennett, 1994). More recent studies have hypothesized that stimuli with different emotional valences would induce different lateralized responses, as also investigated in this thesis. Conspecific vocalizations have been suggested to be processed in the left hemisphere (Hauser and Andersson, 1994) and the palatability of stimuli was

suggested to influence the degree of eye laterality for red-capped mangabeys (deLatude et al., 2009).

Chapter 3 examined the potential influence of stimulus type on eye preference, resulting in a group level eye preference for a high quality food item (bananas), but not for any of the neutral stimuli (such as the empty box, biscuits, and video camera). These results are consistent with previous reports with nonhuman primates where significant laterality was not found for low or non-arousing stimuli (*Cercocebus torquatus torquatus*: de Latude 2009; *Callithrix jacchus*: Hook-Costigan and Rogers 1998; *Otolemur garnettii*: Rogers et al. 1994). Bananas are a known favourite food for the chimpanzees participating in this study, frequently eliciting food barks and visible excitement (hand slapping, bouncing, and play faces), suggesting that they do hold considerable emotional value. For this study the plastic snake also elicited a strong emotional response (alarm calls, whimpering, looking for reassurance). Since snakes are present at the test site, these subjects were familiar with them and have been known to produce fear calls in response to the presence of snakes (Braccini, personal observation).

A direct relationship was previously reported between handedness, fear and exploration in Geoffroy's marmosets, supporting both the Approach-Withdrawal model and the Valence Model (Braccini and Caine, 2009). The Valence Model postulates that the expression and experience of positive emotions are produced in the left hemisphere and negative emotions are processed and expressed through the right hemisphere (Davidson 1992; Ernhart et al. 1998). In the case of eye

preference, a crucial analysis in Chapter 3 shows that the emotional valence of the object does influence the eye used to view it, but only after the subject knew what the object was. In this study we witnessed the subjects approach and initially view an object with one eye, determine the emotional reaction to the object and then take a second look with a different eye. This explains the adjustment in eye use from the initial look to subsequent looks for both of the most emotionally relevant conditions: the snake and banana conditions. These objects elicited the most emotional response of all the objects used, reflecting both positive and negative extremes.

Along similar lines, the Approach-Withdrawal model theorizes that the drive behind approach behaviours are primarily processed in the left hemisphere and withdrawal behaviours are processed in the right hemisphere (Demaree et al. 2005). If an object was repeatedly viewed, or viewed in long duration, the object is apparently not eliciting a negative emotional response worthy of withdrawal or retreat. The opposite might also be true, explaining the shorter total viewing duration, fewer total looks, and significant left-eye preference for viewing the snake; the subjects were actively avoiding looking at the snake and thus activating the right hemisphere. Since a change in eye preference was found from the initial look to subsequent looks for the two most emotionally valuable objects, the data presented in Chapter 3 support both of these theories as emotional valence clearly played a role in eye preference.



More generally, Chapter 2 provides support for theories suggestion that strength of hand preference may increase with arousal in the central nervous system (Larson et al., 1989; Westergaard et al., 1998), because assuming a fully bipedal posture is clearly more difficult for chimpanzees than sitting or standing with arm support.. These results are also consistent with Fagot and Vauclair's (1991) hypothesis that high-level, or difficult, tasks reflect specializations in the brain more accurately than simple low-level tasks. By altering the posture, and possibly the difficulty of the task, the level of emotional arousal may also be affected. The bipedal tool use tasks, especially without any support, were observed to be an uncomfortable and somewhat taxing task for the chimpanzee subjects in this study. This difficulty was reflected by several repeatedly observed behaviours including shaking of legs, and/or reluctance and resistance to performing the task. Thus, the difficulty of the task or the arousal resulting from the difficulty may have driven the increased strength of hand preference observed in chimpanzees.

### **Relationship between hand preference, eye preference and orienting asymmetries**

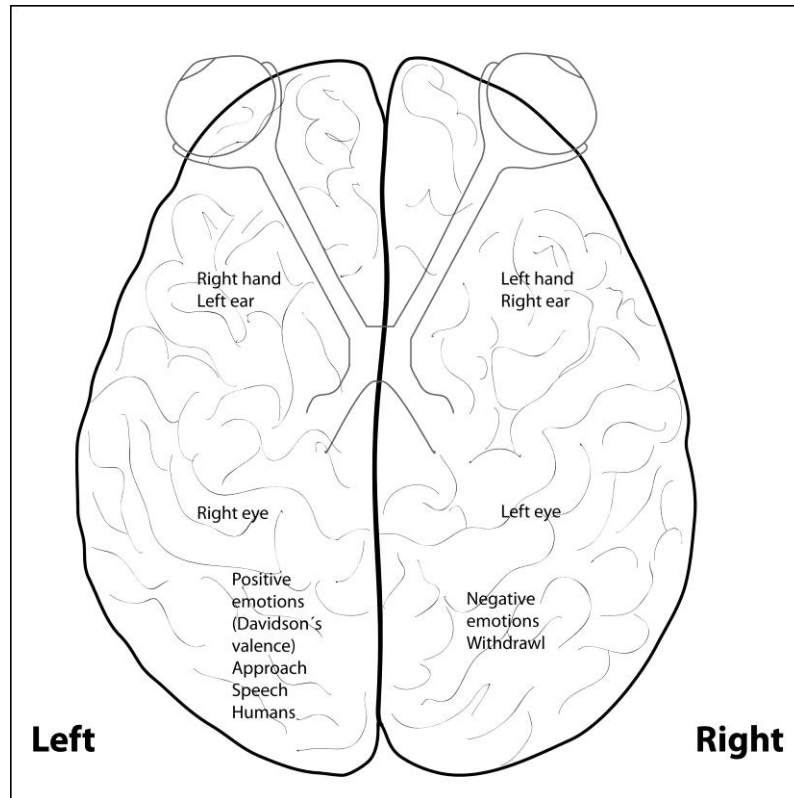
Ideally the same individual subjects would have been used for all studies included in this thesis, allowing for direct comparison across the three measures of laterality. Unfortunately, the housing logistics at the Keeling Centre did not allow for this.

As a result, the same subjects were used for Chapter 2 and 3, allowing for a direct within-subject comparison of eye preference and laterality. Eye index and absolute value eye index from Chapter 2 were compared with handedness measures across

all three postural conditions in Chapter 3. None of the correlations were significant, suggesting that different mechanisms were at work during the expression of these behaviours. Alternatively, the role of arousal and emotion might have overridden any existing relationship between the two lateralized behaviours. Hook-Costigan and Rogers (1996) tested hand, mouth, and eye preferences in marmosets and failed to report significant relationship between these multiple behavioural preferences, concluding that one hemisphere may control feeding and mouth use, while another controls visual preferences and reaching. Currently there is no research indicating a relationship between the multiple behavioural expressions of hemispheric asymmetry in nonhuman primates, which suggests that they might each operate independently.

The research presented in this doctoral thesis examines three lateralized behaviours that are thought to be expressions of hemispheric asymmetry: handedness, eye preference and orienting asymmetry. It is reported in Chapter 2 that bipedalism induced the captive chimpanzees to become significantly more lateralized, but not in any specific direction. Chapter 3 discusses the main effect of stimulus type on the direction of eye preference, number of looks, and looking duration. A left-eye bias was found for viewing the rubber snake and a right-eye bias for viewing the bananas, in addition to a shift in eye preference from the initial look to subsequent looks when viewing the snake. These results suggest an influence of emotion on eye preference. Lastly, a lack of orienting asymmetries is cited in Chapter 4 for conspecific and heterospecific vocalizations. Rather than concluding that head turning is not a valid expression of hemispheric asymmetry, it is hypothesized that

the head turning paradigm is faulty and should not be used without considerable caution.



**Figure 5.1.** Laterality of the brain for controlling hands, ears, eyes, and emotions.

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